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MORPHOLOGY-INFERRED PHYLOGENY AND A REVISION OF THE GENUS *EMMOTUM* (ICACINACEAE)[1]

Rodrigo Duno de Stefano[2] *and Germán Carnevali Fernández-Concha*[2]

ABSTRACT

Emmotum Desv. ex Ham. is a Neotropical, primarily Amazonian and Guayanan genus (Icacinaceae) of 13 tree or shrub species, including a new species here described from Amazonas, Brazil, *E. amazonicum* Duno & Carnevali. A cladistic analysis of the 18 taxa of Icacinaceae including 13 of *Emmotum* was carried out using 41 morphological characters. The single most parsimonious tree shows *Emmotum* as a monophyletic group, strongly supported by nine synapomorphies, with *Poraqueiba* Aubl. as the sister group. In addition, two main groups are identified within *Emmotum*. These two groups laxly correspond with the 1872 classification of Engler: *Emmotum* sect. *Brevistyla* Engl. and *Emmotum* sect. *Longistyla* Engl. (= section *Emmotum*). The genus *Pogopetalum* Benth., synonymous within *Emmotum*, is lectotypified by *P. orbiculatum* Benth. (≡ *E. orbiculatum* (Benth.) Miers). We present a revision of *Emmotum* with information about nomenclature, distribution, ecology, local names, and uses.

Key words: *Emmotum*, Icacinaceae, IUCN Red List, Neotropics, *Pogopetalum*.

Emmotum Desv. ex Ham. is the largest genus of Icacinaceae in the New World. It encompasses 13 exclusively Neotropical species found from northern South America to south-central Brazil and Bolivia. Plants of *Emmotum* are shrubs or trees; the inflorescence is a short panicle, the inner surface of the petals has a conspicuous indument, the ovary is 3-locular (a feature unique in the family), and the fruits are small with a slightly depressed apex.

Emmotum, a name proposed by A. N. Desvaux, was first described by Hamilton (1825). A few years later, Bentham (1841) described *Pogopetalum* Benth., including the two species *P. acuminatum* Benth. and *P. nitens* Benth. He did not make reference to *Emmotum* or to any other genera of the Olacineae.

[1] We would like to thank the Centro de Investigación Científica de Yucatán, A. C. (CICY) for its support. This publication is the partial result of the research conducted by the first author toward the fulfillment of the requirements for his Ph.D. degree. These studies were conducted at the Universidad Complutense of Madrid and the Real Jardín Botánico de Madrid with the collaboration of Dr. Santiago Castroviejo and the support of the Agencia Española de Cooperación (Beca Mutis); we are grateful for all of their support. The senior author acknowledges a grant by the Tinker Foundation scholarship to visit the New York Botanical Garden as well as a grant from the Real Colegio Complutense to visit the Harvard University Herbaria. Special thanks go to two anonymous reviewers, the editorial staff of the *Annals of the Missouri Botanical Garden*, and Gustavo Romero, who improved the paper with comments and suggestions.

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Miers (1852) later described *E. affine* Miers and *E. glabrum* Benth. ex Miers and transferred Bentham's species of *Pogopetalum* to *Emmotum*.

Engler (1872) was the first to propose an infrageneric classification in *Emmotum* with two sections based on attributes of the trichomes on petals, stamens, and ovary. Section *Longistyla* Engl. (= *Emmotum*) was defined by Engler based on the following characters: petals adaxially with red trichomes covering the whole surface, filament of the stamen with the base dilated and the apex attenuate, anthers oblong-ovate with a terete connective, and the style longer than the ovary, whereas section *Brevistyla* Engl. has petals with trichomes at the base and apex, filaments of the stamens with the base and the apex dilated, anthers oblong-linear with the connective fleshy subtetragonous, and the style shorter than the ovary. Engler included *E. glabrum* in his section *Brevistyla* based on a plate published by Miers (1851–1861). This plate, which shows a plant with a short style and stamen with an anther as long as the filament, is more correctly referable to *E. nitens* (Benth.) Miers, and it is this species that is selected as lectotype for section *Brevistyla* (Duno et al., 2007). Engler further assigned *E. orbiculatum* (Benth.) Miers, a species with a short style of less than 0.5 mm long, to section *Longistyla*. Thus, some species assignments were inconsistent with the attributes proposed by Engler to define his sections.

Van Tieghem (1897) described the family Emmotaceae, which he placed close to Icacinaceae, and included the two genera *Emmotum* and *Pogopetalum*. Sleumer (1940) followed Engler's infrageneric division of *Emmotum*, but elevated sections to subgenera. The most complete treatment of *Emmotum* thus far was published by Howard (1942a), in which he proposed four additional species: *E. nudum* R. A. Howard, *E. conjunctum* R. A. Howard, *E. floribundum* R. A. Howard, and *E. fulvum* R. A. Howard. Howard correctly transferred *E. glabrum* to subgenus *Euemmotum* Sleumer, which laxly corresponded to Engler's section *Longistyla*. Howard therefore concluded that the monotypic subgenus *Brevistyla* was of little use and proposed to abandon the infrageneric classification. He was probably unaware that *E. orbiculatum* was better referred to section *Brevistyla*, thus making this bispecific. There are also a few regional treatments of *Emmotum* (Engler, 1872; Carvalho et al., 1973; de Roon, 1994; Howard & Duno de Stefano, 1999), most of which closely followed Howard's (1942a) classification scheme.

Kårehed (2001), using several molecular markers (*ndhF*, *rbcL*, *atpB*, and 18S ribosomal DNA [rDNA]), along with morphological and anatomical evidence, investigated the relationships of Icacinaceae within the Euasteridae I, including a large number of the genera traditionally included within that family. His results conclusively demonstrated that Icacinaceae are polyphyletic with genera scattered across several families and orders. The analyses identified two major clades within a narrowed circumscription of Icacinaceae, now included within the Garryales, in the Asteridae clade (Angiosperm Phylogeny Group, 2009). These were the *Icacina* A. Juss. group, composed mainly of pantropical lianas, and the *Emmotum* group, composed of mostly Neotropical trees, with the exception of *Platea* Blume, a genus with five Asiatic species.

Here we present the results of a cladistic analysis based on morphological characters that address the following questions. (1) Is the genus *Emmotum* monophyletic? (2) If so, what are its synapomorphies and other delimiting characters? (3) What is the position of the genus relative to other Neotropical genera of the *Emmotum* group? (4) What are the phylogenetic relationships among species of *Emmotum*, especially in the context of the infrageneric classification proposed by Engler (1872)?

Materials and Methods

Taxon Analysis

As a result of the taxonomic work of this investigation, 13 species of the genus *Emmotum* are recognized and included as terminal taxa in the ingroup. There are no previous studies exploring the monophyly of *Emmotum*. As mentioned, Kårehed (2001) found the family Icacinaceae not to be monophyletic, and its circumscription was narrowed to include two main groups: the *Icacina* group and the *Emmotum* group. We chose members of this first group as outgroups: *Oecopetalum mexicanum* Greenm. & C. H. Thomps., *Ottoschulzia cubensis* (C. Wright ex Griseb.) Urb., *Poraqueiba paraensis* Ducke, and *P. sericea* Tul. In Kårehed's (2001) study, *Poraqueiba* Aubl. was sister to *Emmotum*, thus supporting the inclusion of this genus as a member of the outgroup. The genera *Oecopetalum* Greenm. & C. H. Thomps. and *Ottoschulzia* Urb. have been mentioned as morphologically and anatomically related to *Emmotum* and *Poraqueiba* (Howard, 1942a, 1942b). The more distantly related Neotropical species *Calatola costaricensis* Standl., a member of the *Emmotum* clade, was used to root the tree. This taxon is characterized by the autapomorphies of dioecious plants, with 4-merous, unisexual flowers (vs. monoecious plants, with 5-merous, bisexual flowers).

Table 1. Continuous morphological characters in the cladistic analysis of *Emmotum*. Letters a, b, c, and d correspond to character states 0, 1, 2, and 3, respectively.

	Character 5, petiole length (cm)	Character 6, lamina length (cm)	Character 9, no. of secondary veins	Character 15, no. of flowers	Character 24, filament length (mm)	Character 28, anther:filament length ratio	Character 32, style length (mm)	Character 37, fruit size (cm)
Calatola costaricensis	2–5, b	10–25, b	6 to 8, b	> 50, c	0, a	5:1, a	0, a	4–7, a
Ottoschulzia cubensis	0.4–0.8, a	2.5–5, a	5 to 8, b	1 to 3, a	ca. 2.5, b	1:1, b	5–5.5, d	2–2.5, a
Oecopetalum mexicanum	(0.7–)1–2, b	10–25, b	5 to 7, b	> 50, c	2.2–3, b	1:1, b	ca. 5, d	1.8–2.2, a
Poraqueiba paraensis	1.5–2, b	10–18, b	4 to 6, b	10 to 20, b	ca. 3.5, b	1:2, c	ca. 0.5, b	5–7, b
P. sericea	2–4, b	15–25, b	7 to 9, b	10 to 20, b	ca. 3.5, b	1:2, c	ca. 0.5, b	6.5–7.5, b
Emmotum acuminatum	(1–)1.5–2, b	8–16, b	6 to 9, b	10 to 20, b	ca. 4, b	1:4, d	3–4, c	ca. 1.5, b
E. affine	(1–)1.5–2.5, b	7–12, b	6 to 9, b	10 to 20, b	3.5–4, b	1:4, d	2.5–3, c	ca. 1.5, b
E. amazonicum	1–1.5, b	7–10, b	11 to 14, b	10 to 20, b	ca. 2, a	1:1, b	ca. 0.5, b	ca. 1.5, b
E. celiae	0.4–0.8, a	2–5, a	2 to 3, a	10 to 20, b	2.2–3, b	1:4, d	3–4, c	ca. 0.8, b
E. conjunctum	(1–)1.2–2, b	8–12, b	9 to 13, b	10 to 20, b	4–4.5, b	1:4, d	3–4, c	ca. 1.5, b
E. fagifolium	1–2, b	6.5–18, b	6 to 9, b	10 to 20, b	3.5–4, b	1:4, d	2.5–3.5, c	ca. 1.5, b
E. floribundum	1.5–2.5, b	8–14, b	8 to 11, b	10 to 20, b	4.5–5, b	1:4, d	3.5–4, c	ca. 1.5, b
E. fulvum	ca. 1.5, b	10–16, b	6 to 9, b	10 to 20, b	4.5–5, b	1:4, d	3–3.5, c	ca. 1.5, b
E. glabrum	0.5–0.8(−1), a	5–13, a	2 to 5, a	10 to 20, b	2.8–3, c	1:4, d	2.5–3, c	ca. 1.5, b
E. harleyi	1.3–1.5, b	5–10, a	9 to 11, b	10 to 20, b	1.5–1.8, a	1:1, b	ca. 0.5, b	1–1.2, b
E. nitens	1.5–2.5, b	(5–)6–12, b	6 to 8, b	10 to 20, b	1.5–2, a	1:1, b	ca. 0.5, b	ca. 1.5, b
E. orbiculatum	1–2, b	10–20, b	8 to 9, b	10 to 20, b	ca. 2, a	1:1, b	ca. 0.5, b	ca. 1.5, b
E. yapacanum	0.5–0.8, a	6–7, a	2 to 3, a	5 to 10, b	2.5–4, c	1:4, d	2.5–3, c	ca. 1.5, b

Table 2. Data matrix used in the cladistic analysis of *Emmotum*.

Calatola costaricensis	021011x01100002l0?120?3003?03300001000020
Ottoschulzia cubensis	000000200001110001000?120111230300011000
Oecopetalum mexicanum	001011001101112001100?120111230300001200
Poraqueiba paraensis	011111001101211001100?020001000100000000
P. sericea	011111001101211001100?020001000100000000
Emmotum acuminatum	012111x01101211010111022121232121l0111111
E. affine	x12111011101211010111022021232020111111111
E. amazonicum	012111211101211010111121022141010l0111111
E. celiae	112100200001211010111022021232020111111111
E. conjunctum	x12111x11111211010111022021232020111111111
E. fagifolium	012111x01101211010111022021232020111111111
E. floribundum	012111211111211010111022121232121l0111111
E. fulvum	012111x11111211010111022021232020111111111
E. glabrum	x12100100001211010111022021232020111111111
E. harleyi	012111011111211010111121022141010l0111111
E. nitens	012111011111211010111121022141010111111111
E. orbiculatum	012111211111211010111121022141010111111111
E. yapacanum	112100100001211010111022021232020111111111

x = polymorphic character 0,1; ? = not applicable character.

SAMPLING

A morphological data matrix was obtained after careful examination of more than 200 herbarium specimens of *Emmotum* and the outgroup taxa from the following 25 herbaria: A, AAU, BM, CAS, ECON, F, G, GH, INPA, K, LBP, MA, MER, MEXU, MICH, MO, MY, NY, PMA, PORT, S, SCZ, US, VEN, and XAL. Specimens examined included the types of all described terminal taxa.

CHARACTERS AND CODING

Forty-one morphological characters were obtained from general vegetative and reproductive morphology. Most characters were discrete, but a few were continuous, namely petiole length (character 5), lamina length (character 6), number of secondary veins (character 9), number of flowers (character 15), length of the filament (character 24), anther:filament length ratio (character 28), style length (character 32), and fruit size (character 37), which were transformed (binary or multistate) by identification of conspicuous gaps in the interspecific variation of the taxa (Table 1). All characters used in the analysis are listed and described in Appendix 1, and the data matrix is presented in Table 2. All characters were similarly weighted, and multistate characters were considered as unordered (nonadditive, Fitch parsimony [Fitch, 1971]).

Terminology follows the Systematic Association Committee for Descriptive Biological Terminology (1962) for leaf shape and apex (characters 7, 23, 26, and 36). The trichome terminology used in this study (characters 3, 4, and 21) has been compared with a major survey of Icacinaceae (Heintzelman & Howard, 1948). There is a wealth of anatomical and pollen information for the family (see Kårehed, 2001, for bibliography), but most of these characters turned out to be noninformative in the context of the ingroup-outgroup relationships herein.

PHYLOGENETIC ANALYSES

The phylogenetic analyses were performed with the program NONA (Goloboff, 1993) in conjunction with a WinClada shell (Nixon, 2002). The parsimony ratchet algorithm (Nixon, 1999) was implemented to optimize the parsimony search with the following settings: number of iterations/repetitions = 200 and number of trees to hold/iteration = 1. Support for the clades recovered from the analyses was estimated with the use of 1000 jackknife iterations (JK) and the following search parameters: 30 search replicates (mult*30), three starting trees per replication (hold/3), and maximum number of trees set to 25,000. Additional support for these clades was evaluated with the use of the Bremer index or Bremer decay index (Bremer, 1988) with the following parameters: 20,000 trees as maximum number held in memory (h 20000), the longest of them 10 steps longer than the most parsimonious trees (with the implementation of the bootstrap [BS] 10 command).

Results

CLADISTIC ANALYSIS

Of the 41 characters originally explored, the number of flower parts (character 12), sexuality of the flower (character 14), sepal aestivation (character 16), and

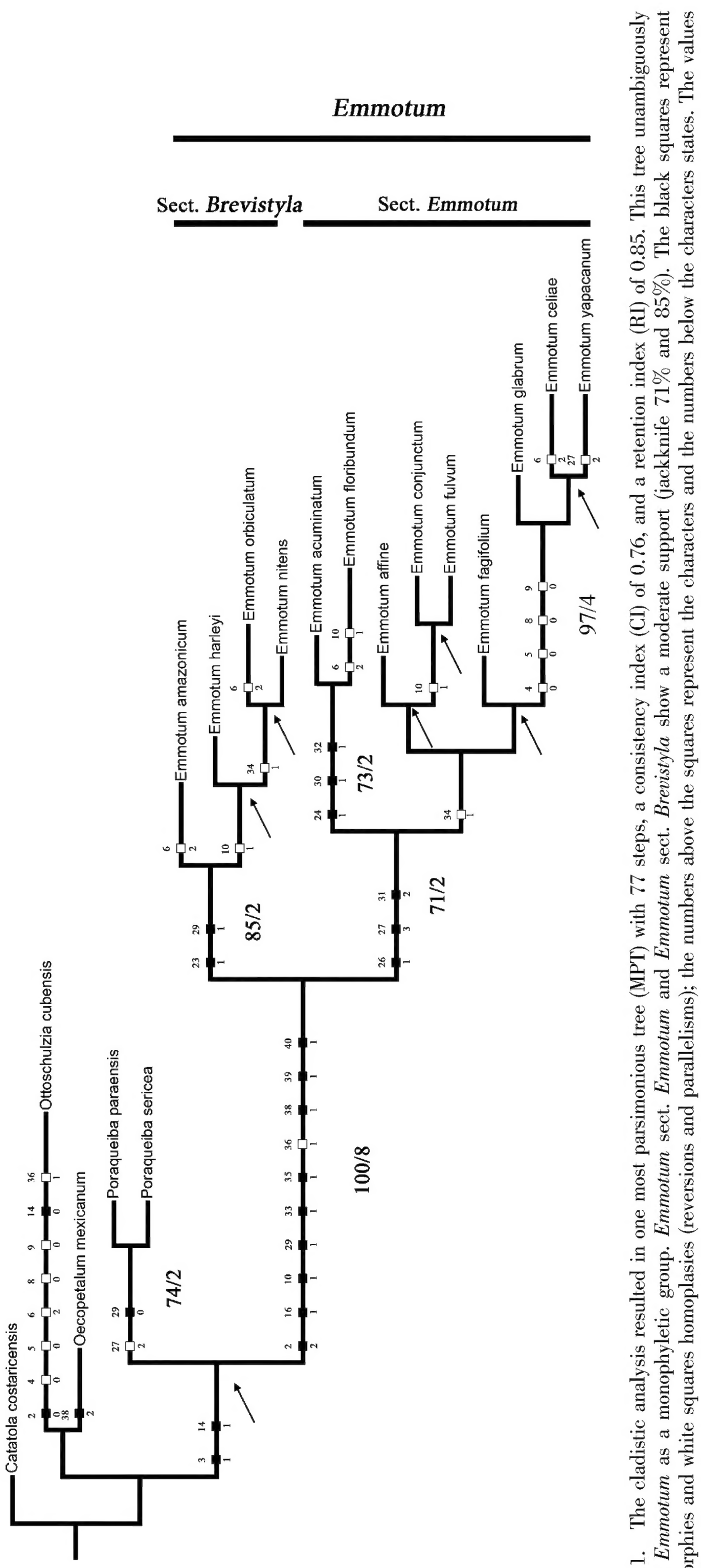

Figure 1. The cladistic analysis resulted in one most parsimonious tree (MPT) with 77 steps, a consistency index (CI) of 0.76, and a retention index (RI) of 0.85. This tree unambiguously identifies *Emmotum* as a monophyletic group. *Emmotum* sect. *Emmotum* and *Emmotum* sect. *Brevistyla* show a moderate support (jackknife 71% and 85%). The black squares represent the characters and the numbers above the squares represent the characters states. The values synapomorphies and white squares homoplasies (reversions and parallelisms); the numbers below different branches represent the jackknife values and the Bremer index or Bremer decay index. The black arrows show clades without support.

petal connation (character 19) were not phylogenetically informative (12% of the original data). These characters were thus excluded from consecutive analyses. The cladistic analysis resulted in a single most parsimonious tree (MPT) of 77 steps, with a consistency index (CI) of 0.76 and a retention index (RI) of 0.85. The single MPT obtained (Fig. 1) unambiguously identifies *Emmotum* as a highly supported (JK = 100%, BS = 8) monophyletic group with nine synapomorphies and *Poraqueiba* as the sister taxon, with which it shares two synapomorphies.

Discussion

Robustness of the phylogenetic hypothesis

Similar morphological analyses at the species level show a similar number of morphological and/or anatomical informative characters, e.g., *Asarum* L. with 32 taxa (ingroup) and 37 characters (Kelly, 1997) and *Monsonia* L. with 25 taxa (ingroup) and 20 characters (Aldasoro et al., 2001). Some other analyses, with more characters, attempt to resolve relationships at the species and generic levels (e.g., Schulman & Hyvönen, 2003, for the genus *Adelobotrys* DC., Melastomataceae). In this case, the data matrix included up to 117 morphological characters (91 informative). This high number of characters is due to the inclusion of a large number of outgroup taxa, up to 10 species in seven different genera, thus increasing the number of informative characters. The inclusion in our analysis of some lianoid genera such as *Casimirella* Hassl., *Leretia* Vell., or *Mappia* Jacq. could result in the addition of new morphological, anatomical, and palynological informative characters. However, the inclusion of these characters, although providing better resolution at the base of the tree, would increase neither the resolution nor the support to the taxa and clades in the ingroup, which is our main focus. It is unlikely that many additional, informative macromorphological characters could be discovered, rendering the search of micromorphological or molecular data necessary to provide further resolution of species relationships.

The CI of the single MPT, 0.76, falls near the higher end of the range normally obtained in similar, morphology-based analyses (Sanderson & Donoghue, 1989). These ranges of the CI indicate a moderate level of homoplasy. The topology of the consensus tree, and character states with unambiguous optimization supporting relevant clades, are described below.

Monophyly of *Emmotum*

At the base of the single MPT, the clade formed by *Ottoschulzia cubensis* and *Oecopetalum mexicanum* appears as sister to a clade comprising the genera *Poraqueiba* and *Emmotum*. *Ottoschulzia cubensis* shows two autapomorphies: malpighiaceous hairs with unequal arms (character 3) and inflorescences with one to three flowers (character 15). There is also one autapomorphy for the genus that appears as non-informative: the petal joined at the base (character 19). For *Ottoschulzia* there are also other vegetative and floral character states that represent revertions (e.g., a reduction in the size of the petiole [character 5] and the lamina [character 6], type of apex [character 7], few, nonconspicuous secondary veins [characters 9 and 10], and small fruits [character 37]). On the other hand, the genus *Oecopetalum* shows one autapomorphy, fruits with an acute apex (character 39), but this genus also shows several other unique floral characters that were not included in the analysis (e.g., persistent calyx, petals with prominent midrib [unlike those of *Poraqueiba*], and the anthers with lateral dehiscence). The inclusion of these characters (see Greenman & Thompson, 1914; Howard, 1942b) would not affect the topology, resolution, or support for the tree because they are autapomorphic.

The status of *Poraqueiba* as sister taxon to *Emmotum*, as inferred by Kårehed (2001), is supported by our results. Both genera have Amazonian or Guayanan distributions, while the other outgroups have Antillean and Central American distributions; two synapomorphies support this clade, namely articulated hairs (character 4) and number of flowers (character 15).

Phylogeny of *Emmotum*

Emmotum is easily diagnosable and strongly supported by nine synapomorphies: red pigmentation of tissues upon pickling (character 2); white flowers (character 17); slightly developed petal texture (character 20); petals with cylindrical hairs (character 21); multilocular ovary (character 34); fruits small, less than 1.5 cm long (character 37), and with the apex shortly mucronate (character 39); slightly developed endocarp (ch. 40), and seed with a relatively large embryo (character 41).

Within *Emmotum*, two clades are identified. These clades correspond to Engler's (1872) sections, later reprised as Sleumer's (1940) subgenera. The first clade corresponds to *Emmotum* sect. *Brevistyla* (JK = 85%, BS = 2) and consists of four species found only south of the equator, principally in Brazil. *Emmotum orbiculatum* is from the Brazilian states of Amazonas and Pará, representing the northernmost member of this clade. *Emmotum nitens* grows in the cerrado of Brazil to Minas Gerais and Bolivia and is the most

austral taxon of the clade. Two sets of populations formerly referred to *E. nitens* deserve recognition as separate species—*E. amazonicum* Duno & Carnevali, described below, is restricted to the state of Amazonas, Brazil, where it is partially sympatric with *E. orbiculatum*, while *E. harleyi* Duno is restricted to the Chapada Diamantina in Bahia, Brazil (Duno et al., 2007). This Brazilian clade is characterized by two synapomorphies: filaments 1.5–2 mm long (character 24) and the stamen connective slightly developed (character 30). These four taxa feature discontinuous indument with only two clusters of hairs (character 22), one at the base and another at the apex of the adaxial surface, but the character is not applicable to any member of the outgroup.

The second clade corresponds to *Emmotum* sect. *Emmotum* and includes nine species (JK = 71%, BS = 2). The clade is characterized by three synapomorphies: the apex of the filament dilated (character 27), the anther three or four times longer than the filament (character 28), and the style 2.5–4 mm long (character 32). As here circumscribed, this clade corresponds to those species with densely lanate petals, stamens with filaments dilated at the base and attenuate at the apex, and the anthers ovate. This second clade includes the generitype, *E. fagifolium* Desv. ex Ham.

Within *Emmotum* sect. *Emmotum*, a clade made up of *E. acuminatum* (Benth.) Miers and *E. floribundum* (JK = 73%, BS = 2) is sister to the rest of the taxa. They have three synapomorphies: a dorsifixed anther (character 25), a diminute ring of tissue around the base of the ovary (character 31), and lateral styles (character 33). Another clade contains two subclades, one containing *E. conjunctum* R. A. Howard and *E. fulvum*, and another containing the other five species. On the other hand, *E. affine* is sister to *E. conjunctum* and *E. fulvum*. These two taxa are not supported by any synapomorphy but by one character state reversion, a lamina with caducous pubescence (character 11). Both species occur on sandstone-derived substrates of the Guayana Region, but *E. fulvum* inhabits low, medium to tall forests on tepui slopes between 850 and 1700 m, while *E. conjunctum* grows in several kinds of savanna associations and forests, between 300 and 1400 m. *Emmotum fagifolium* is the sister taxon of a clade including three Guayanan species, *E. glabrum*, *E. celiae* R. A. Howard, and *E. yapacanum* R. A. Howard (JK = 97%, BS = 4) with four reversions: short petioles, 0.4–0.8 cm long (character 5), a small lamina, 2–5 cm long (character 6), lamina with only two or three pairs of secondary veins (character 9), and inconspicuous secondary veins (character 10).

EVOLUTION OF SELECTED CHARACTERS

Petals

In the genus *Poraqueiba* the petals are fleshy and glabrous with two internal furrows separated by a usually well-developed median ridge. *Emmotum*, on the other hand, has petals slightly fleshy (character 20), densely indumented with cylindrical hairs (character 21), and lacking internal furrows and ridge.

Stamens

In the *Emmotum* group of the Icacinaeae, the transformation of the stamens is one of the most relevant evolutionary trends. In *Poraqueiba*, the stamens have fleshy, thickened filaments and anthers with wide, elongated connectives. An examination of the evolution of the features associated with the androecium in *Emmotum* indicates a trend toward an elongation of these parts. In *Emmotum* sect. *Brevistyla*, the stamens are similar to those of *Poraqueiba* but with thinner connectives, anthers, and filaments. In *Emmotum* sect. *Emmotum*, the stamens become thin and longer, and the connective becomes ovate with no prolongation. The analysis shows that the different characters associated with the stamen morphology are involved in the topology of the single MPT. For example, *Poraqueiba* is supported by two characters (27 and 29) from stamen morphology and *Emmotum* sect. *Emmotum* is also defined by a synapomorphy associated with these characters (28). Also, in *Emmotum* sect. *Emmotum*, another clade (*E. acuminatum* and *E. floribundum*) is supported by a stamen character (25); in this case, the anthers become dorsifixed. We believe many of these stamen's characters are strongly correlated, e.g., relative size of the filament and the anther, shape of the anther, and shape and prolongation of the connective.

Ovary

One of the most important characteristics of the genus *Emmotum* is the multilocular ovary (character 34), which is not found in any other Icacinaceae. Another important character is the length of the style (character 32). There is a trend toward an elongation of the style in the evolution of the *Emmotum* group. *Poraqueiba* has an inconspicuous style; in *Emmotum* sect. *Brevistyla*, the style is slightly longer, while it is longest in *Emmotum* sect.

Emmotum. The clade *E. acuminatum–E. floribundum* is characterized by a shift in the style from a central to a lateral position (character 33) while its surface becomes glabrous, a reversal to a more ancestral character state found in the other genera of the *Calatola–Oecopetalum–Poraqueiba* clade (although glabrous in *Calatola* Standl.).

Vegetative characters

The most obvious vegetative changes occur in the clade composed of *Emmotum celiae*, *E. glabrum*, and *E. yapacanum*. In this group, and according to our results, at least five evolutionary changes in the leaves have occurred. These changes involve a decrease in petiole length (character 5) and an overall reduction in the size of the lamina (character 6). Furthermore, the number of secondary veins is drastically reduced (character 9) and poorly developed (character 10). It remains to be addressed whether these changes are adaptations to the more restrictive conditions of the tepui summit habitats.

Taxonomic Synopsis

I. Emmotum Desv. ex Ham., Prodr. Pl. Ind. Occid. (Hamilton): 29. 1825. TYPE: *Emmotum fagifolium* Desv. ex Ham.

Trees or shrubs with decumbent branches, up to 5–20(–30) m high, generally all parts pubescent, the indument gray to ferruginous or golden, articulated, erect, rarely undulate, variable in length, generally appressed. *Leaves* alternate, coriaceous or subcoriaceous, generally bicolored, green to golden on the abaxial surface and dark green and lustrous on the adaxial surface; lamina narrowly ovate, ovate, narrowly elliptic, elliptic to nearly orbicular, apex acuminate, acute, or mucronate, rarely retuse, base acute, obtuse, or attenuate, margin entire, slightly revolute; secondary veins in 2 to 14 pairs, variously developed, alternate, free near the margins or joined together in a series of marginal loops; abaxial surface glabrous, sericeous to velvety, rarely tomentose, hairs caducous to persistent; petiole to 2.5 cm, canaliculate, a nitid line of abscission at the base, puberulent, sericeous, or velvety, rarely glabrescent. *Inflorescence* axillary, paniculate, to 5 cm, pedicels short, articulated apically, sericeous or densely sericeous. Bracts triangular or widely triangular, slightly concave, sericeous outside, glabrous within. *Flowers* pentamerous, actinomorphic, bisexual, hypogynous, fragrant; bracteoles 1 or 2 per flower, subtriangular to triangular, concave, sericeous outside and glabrous within; pedicels to 3 mm, sericeous to densely sericeous; *calyx* campanulate, fleshy, lobes broadly triangular to triangular, sericeous outside, glabrous within, apex acute, margin entire; *corolla* with the petals free, white, obovate, oblong, or narrowly oblong, sericeous outside, rarely glabrous, densely lanate within, sometimes 2 clusters of trichomes at the base and the apex; margin entire; apex acute, reflexed; main vein patent within; *stamens* with fleshy, flattened, erect, glabrous filaments, base dilated, apex dilated or attenuate; anthers tetragonous or cordate, attached basally, rarely dorsally, longitudinally dehiscent; connective ovate or elliptic, sometimes prolongated beyond anther thecae; *gynoecium* surrounded by a well-developed ring of glabrous tissue at the base of the ovary, a true disk absent; *pistil* with the ovary globose, hirsute or glabrous, 2- or 3-locular; style central, sometimes eccentric, long, rarely very short; stigma capitate, rarely 3-lobed. *Fruits* subglobose, exocarp very thin, green when immature and yellow to black when mature; mesocarp thin; endocarp hard, with 3 poorly developed ribs; seeds in general 1, rarely 2 to 3.

Etymology. Miers (1852) mentioned that he did not know the origin of the name, but suggested that it comes from the Greek ευ (prefix meaning "well") and μοτος (linen cloth), in reference to the densely lanate inner surface of the petals.

Discussion. Van Tieghem's (1897) lectotypification of the genus *Pogopetalum* (published in 1841) with *P. nitens*, described in 1843, is untenable because this species is not part of the protologue of the genus (McNeill et al., 2006: Art. 9.10, 10.1). Bentham originally cited two species for the genus in 1839: *P. orbiculatum* and *P. acuminatum*. The generic diagnosis of *Pogopetalum* features characters attributable to both species, but the plate (tab. XLII) can be unambiguously referred to *P. orbiculatum*, which was the only member of *Emmotum* sect. *Brevistyla*, based on its short style and characters of the stamens similar to those of other members of *Emmotum* sect. *Brevistyla*.

Key to the Sections of *Emmotum*

1a. Filaments basally dilated, apically attenuated; anthers oblong-linear; connective ovate; ovary with a long style, 2–5 mm long ..... *Emmotum* sect. *Emmotum*

1b. Filaments dilated both basally and apically; anthers oblong; connective elliptic and prolongated; ovary with a short style, less than 0.5 mm long ..... *Emmotum* sect. *Brevistyla*

KEY TO THE SPECIES OF *EMMOTUM*

1a. Lamina with secondary veins poorly developed, with 2 to 5 pairs of veins; mostly glabrous when mature.
  2a. Lamina 2–5 × 1.1–3 cm, obovate, the apex acute or rounded, slightly mucronate, the base attenuate, 2 or 3 pairs of secondary veins ..... *E. celiae*
  2b. Lamina 5–13 × 3–4.5 cm, ovate or elliptic, the apex short- or long-acuminate, the base acute-attenuate, 2 to 5 pairs of secondary veins.
    3a. Peduncle of the inflorescence less than 1.5 cm long ..... *E. glabrum*
    3b. Peduncle of the inflorescence ca. 3 cm long..... *E. yapacanum*
1b. Lamina with secondary veins well developed or covered with a dense indument, with 5 to 14 pairs of veins; pubescent or glabrous when mature.
  4a. Petals adaxially with only clusters of hairs at the base and the apex, more rarely the hairs laxly continuous from base to apex; style less than 1 mm long (section *Brevistyla*).
    5a. Lamina densely tomentose on the abaxial surface; petals sparsely lanate adaxially along the main vein; ovary glabrous ..... *E. harleyi*
    5b. Lamina with indument of variable density on the abaxial surface; petals with clusters of trichomes at the base and the apex alone; ovary hirsute, rarely glabrous.
      6a. Lamina broadly elliptic to suborbicular ..... *E. orbiculatum*
      6b. Lamina narrowly ovate to elliptic-oblong.
        7a. Lamina elliptic to elliptic-oblong, 11 to 14 pairs of secondary veins, dark brown, abaxial surface puberulent, brown-yellow; ovary glabrous..... *E. amazonicum*
        7b. Lamina narrowly ovate, ovate, elliptic to elliptic-oblong, fewer than 9 pairs of secondary veins, dark green to dark yellow, occasionally dark brown, abaxial surface villose, yellow, ocasionally brown-yellow; ovary hirsute ..... *E. nitens*
  4b. Petals densely lanate adaxially; style long, 2.5–4 mm long.
    8a. Ovary hairy, the style central.
      9a. Lamina bicolored, abaxial surface densely velvety with long, slightly undulate trichomes ... *E. fulvum*
      9b. Lamina concolorous, abaxial surface glabrous, sericeous, or tomentose.
        10a. Lamina elliptic, 7–12 × 3–7 cm; 6 to 9 pairs of secondary veins ..... *E. affine*
        10b. Lamina oblong, elliptic, or ovate, 6.5–18 × 3–8 cm; 7 to 13 pairs of secondary veins.
          11a. Abaxial surface of the lamina slightly pubescent with very short trichomes; the secondary veins free at the end, 9 to 13 pairs of secondary veins..... *E. conjunctum*
          11b. Abaxial surface of the lamina almost glabrous; the secondary veins joined together in a series of marginal loops, 6 to 9 pairs of secondary veins ..... *E. fagifolium*
    8b. Ovary glabrous, the style lateral.
      12a. Lamina ovate or oblong, drying dark brown, chestnut, or tan abaxially; secondary veins 6 to 9 pairs, abaxial surface glabrous; the apex acuminate ..... *E. acuminatum*
      12b. Lamina elliptic or orbiculate, drying green-brown; secondary veins 8 to 11 pairs, abaxial surface sericeous; the apex acute or mucronate ..... *E. floribundum*

Ia. Emmotum Desv. ex Ham. sect. **Emmotum**. *Emmotum* sect. *Longistyla* Engl., Fl. Bras. (Martius) 12(2): 44. 1872. *Emmotum* subg. *Euemmotum* Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 15: 233. 1940. TYPE: *Emmotum fagifolium* Desv. ex Ham.

Emmotum sect. *Emmotum* is characterized by the flowers with the petals densely lanate within; stamens with the filament dilated at the base, but the apex attenuate; the anthers oblong to linear; and the ovary with a long style, exceeding 1 mm, that is centric or eccentric in position. This section includes the following nine species: *E. acuminatum*, *E. affine*, *E. celiae*, *E. conjunctum*, *E. fagifolium*, *E. floribundum*, *E. fulvum*, *E. glabrum*, and *E. yapacanum*.

1. Emmotum acuminatum (Benth.) Miers, Ann. Mag. Nat. Hist., ser. 2, 10: 178. 1852. Basionym: *Pogopetalum acuminatum* Benth., Proc. Linn. Soc. London 1(10): 88. 1841 [6 Apr. 1841]. TYPE: Brazil. Amazonas: growing on the high banks of the Rio Negro, *R. Schomburk 970a* (holotype, K!; isotypes, F!, G!, K!, P not seen, US!).

Emmotum nudum R. A. Howard, J. Arnold Arbor. 23: 485, tab. I. 1942. TYPE: Brazil. Pará: Faro, "in campis arenons loco Tigre," 31 Dec. 1929, *A. Ducke 11367* (holotype, US!; isotypes, K!, U not seen).

Shrubs or trees, to 20 m. *Leaves* coriaceous, not bicolored, dark brown-green on both surfaces; lamina 8–16 × 3–9 cm, oblong to ovate, rarely elliptic, apex slightly acuminate to acute, base rounded or slightly obtuse, puberulent on the abaxial surface, glabrous on the adaxial surface; secondary veins 6 to 9 pairs, conspicuous; petiole (1–)1.5–2 cm. *Inflorescences* axillary, 1- to 5-floriferous branches, to 3 cm; *calyx* campanulate, sepal lobes ca. 1 × 0.8 mm, triangular; *corolla* with white petals, 4–5 × 1.2–1.5 mm, narrowly oblong, densely pilosulose, forming a beard on the adaxial surface; *stamens* 4–5 mm, filaments ca. 4 mm, slightly swelled; anthers dorsifixed, connective

ovate; *pistils* 5–5.5 mm, ovary glabrous; style 3–4 mm, eccentric. *Fruits* ca. 1.5 × 1.5 cm (diam.).

Distribution and ecology. *Emmotum acuminatum* is known from Venezuela (Amazonas), Guyana (Cuyuni-Mazaruni), and Brazil (Amazonas, Pará, Rondônia, and Roraima). It grows in forests and savannas at elevations between 50 and 120 m.

Phenology. *Emmotum acuminatum* flowers between October and July and fruits between March and December.

IUCN Red List category. Given its distribution in Amazonian Brazil and the Guianas (Venezuela and Guyana), this species is listed as Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Discussion. In the phylogenetic analysis, *Emmotum acuminatum* is the sister species of *E. floribundum*. Both species share the following synapomorphies: dorsifixed anthers and ovary glabrous with a long, eccentric style. In addition, they grow sympatrically in part of their distribution.

Additional specimens examined. BRAZIL. **Amazonas:** Manaus, Igarapé do Franco, *Chagas 3578* (A); rio Trombetas, margem direita ao norte da Mineraçao St. Patricia, campina do Monte Branco, *C. A. Cid Ferreira et al. 1464* (A, NY); Boca do Río Araririrá, margem direita do río Negro, *C. A. Cid Ferreira 9283* (GH, NY); Manaus, loco Cachoeira Grande, *A. Ducke 376* (A, MO, NY, R); Manaus, Estr. Aleixo, *A. Ducke 2012* (A, GH, NY, R, US); BR156, betw. Calçoene & Rio Amapá Grande, ca. 35 km S of Calçoene, *B. V. Rabelo et al. 2994* (A, F, MO, NY, US); Manaus, Igarapé do Parque 10, *Pessoal do CPF 6158* (A); Secus Rio Negro, inter Barcellos & San Isabel, *R. Spruce 1969* (NY [photo]); Secus Rio Negro, inter Barcellos & San Isabel, *R. Spruce 1989* (G, K, MO, US [photo]). **Pará:** Ilha do Marajo, Sitio Campina, on river Pracuuba-mirim, ca. 1 hr. by boat upstream from São Sebastião de Boa Vista, *G. L. Sobel et al. 4558* (MO). **Rondônia:** Igarpé Preto, *B. G. S. Riberiro 1085* (A). **Roraima:** Rio Xeriuini, *J. M. Pires et al. 13994* (A, INPA); Río Branco, margen esquedrada do Paraná do Marará, *M. R. Santos 141* (NY). GUYANA. **Cuyuni-Mazaruni:** Kukenan River, *Schomburgk 970* (K [2], F [photo], G, GH, MO [photo], NY [photo], US). VENEZUELA. **Amazonas:** Río Guainía, just S of Maroa, *B. Maguire & J. J. Wurdack 36439* (A, NY, VEN); along river just above Tamatama, *J. J. Wurdack & L. S. Adderley 43120* (GH, NY, VEN).

2. Emmotum affine Miers, Ann. Mag. Nat. Hist., ser. 2, 10: 180. 1852. TYPE: Brazil. Brasilia, s.d., *F. Sellow s.n.* (holotype, K!).

Shrubs and trees, 4–10 m. *Leaves* coriaceous, sharply bicolored, green-grayish on the abaxial surface, dark green and shiny on the adaxial surface; lamina 7–12 × 3–7 cm, elliptic to ovate, apex slightly acuminate to acute, base rounded or slightly obtuse, sericeous on the abaxial surface, glabrous on the adaxial surface; secondary veins 6 to 9 pairs, conspicuous; petiole (1–)1.5–2.5 cm. *Inflorescences* axillary, (1)3- to 4(5)-floriferous branches, up to 4 cm. *Flowers* pentamerous; pedicels 3 mm; *calyx* campanulate, sepal lobes ca. 1 × 0.8 mm, triangular; *corolla* with petals white, 4.5–5 × 1.2–1.5 mm, narrowly oblongate, densely pilosulose, forming a beard on the adaxial surface; *stamens* 4–4.5 mm, filaments 3.5–4 mm, slightly swelled; anthers basifixed, connective ovate; *pistils* 3.5–4.5 mm, ovary hirsute; style 2.5–3 mm, terminal. *Fruits* ca. 1.5 × 1.5 cm (diam.).

Distribution and ecology. *Emmotum affine* is endemic to the northeastern coast of Brazil, in Bahia, Espírito Santo, Pernambuco, and Sergipe. It grows in the coastal forest (restinga) in sandy soils between 0 and 50 m elevation.

Phenology. *Emmotum affine* has been collected in flower in October to July and in fruit in December to July.

IUCN Red List category. *Emmotum affine* does have a wide distribution (northeast Brazil). However, it grows in one of the most threatened ecosystems in Brazil, the Mata Atlântica, and it is therefore listed as Vulnerable (VU), according to IUCN Red List criteria (IUCN, 2001).

Discussion. *Emmotum affine* is a shrub or small tree from the Brazilian restinga. In the phylogenetic analysis it emerges as sister species to a clade with two species, *E. conjunctum* and *E. fulvum*. However, from a phenetic point of view it is more similar to *E. fagifolium*. It differs from *E. fagifolium* in its ovate to elliptic lamina (vs. ovate to oblong, sometimes elliptic), apiculate or acute apex (vs. long acuminate to acute), and the sericeous indument on the abaxial surface (vs. glabrous).

Additional specimens examined. BRAZIL. **Bahia:** Maraú a Ubaitaba, *J. Almeida & T. S. Santos 107* (A, NY); Maraú, *R. P. Belém & R. S. Pinheiro 3042* (A [3], NY); Santa Cruz Cabrália, *R. P. Belém & R. S. Pinheiro 3305* (A [3], NY); Parque Nacional Monte Pascoal, *S. G. da Vinha & T. S. Santos 968* (A, NY); 65 km NE of Itabuna, at mtn. of Rio de Contas on N bank, opposite Itacaré, *R. M. Harley et al. 18388* (K, MO); 11 km S of Santa Cruz Cabrália, *R. M. Harley et al. 17055* (A, NY, US); Copuva, *G. Hatschbach & J. M. Silva 48754* (MO, US); rd. BA 001, trecho Alcobaça/Prado, a 5 km a NW de Alcobota, *S. A. Mori et al. 10577* (A, K, NY); Rodovia BR 030, trecho Ubaitaba/Maraú, 45–50 km a leste de Ubrita, *S. A. Mori et al. 11971* (A, NY); rd. BR 500, 18.7 km ao N de Santa Cruz de Cabrália, *S. A.*

Mori et al. 12122 (A, US); BA-099 Estrada do Côco, Guarajuba, Reserva Ecol., *G. C. P. Pinto & H. P. Bautista 315/83* (K, NY); Barrolândia, Est. Exper. Gregorio Bondar, CEPLAC, 48 km E of BR 101 on rd. to Belmonte, *W. W. Thomas et al. 9875* (A, NY). **Espírito Santo:** lago do Milho, *A. L. Peixoto et al. 333* (US); 6 km N of Guarapari, *W. W. Thomas et al. 6101* (NY). **Pernambuco:** Prazeres, Tapera, *B. Pickel 3125* (A, F, US). **Sergipe:** ca. 2 km do Distr. Crasto, na estrada Sta. Luzia do Itanhi, *S. C. Sant'Ana et al. 422* (NY).

3. Emmotum celiae R. A. Howard, Mem. New York Bot. Gard. 29: 63, fig. 55. 1978. TYPE: Venezuela. Amazonas: Serranía Yutaje, Río Manapiare, Cerro Yutaje, 21 Feb. 1953, *B. Maguire & C. Maguire 35351* (holotype, NY!; isotypes, A!, US!). Figure 2.

Shrubs or tree, to 10 m. *Leaves* subcoriaceous, nonbicolored, dark brown-green in both surfaces; lamina 2–5 × 1.1–3 cm, obovate, apex acute or rounded, slightly mucronate, base attenuate, glabrous on both surfaces; secondary veins 2 to 3 pairs, inconspicuous; petiole 0.4–0.8 cm. *Inflorescences* axillary, 1- to 3-floriferous branches, up to 2 cm; peduncle short, no longer than 1 cm. *Flowers* pentamerous; *calyx* campanulate, sepal lobes ca. 1 × 0.8 cm, triangular; *corolla* with the petals white, 3–3.5 × ca. 1 mm, narrowly oblong, densely pilosulose, forming a beard on the adaxial surface; *stamens* 3.2–3.5 mm, filaments 2.2–3 mm, slightly swelled; anthers ca. 1.2 mm, basifixed, connective ovate; *pistils* 5–5.5 mm, ovary hirsute; style 3–4 mm, eccentric. *Fruits* ca. 0.8 × 0.6 cm (diam.).

Distribution and ecology. *Emmotum celiae* is endemic to Venezuela, where it has been collected in the northern portion of Amazonas State. It grows in shrublands, low forests, or exposed rocky areas on top of the sandstone plateau of Cerro Yutaje, between 500 and 2000 m elevation.

Phenology. *Emmotum celiae* has been collected in flower and fruit in January and May.

IUCN Red List category. *Emmotum celiae* is only known from a few collections. Without further information, it is best listed as Data Deficient (DD) according to IUCN Red List criteria (IUCN, 2001). However, because it is restricted to isolated sandstone table mountain slopes and summits in a completely inaccessible area, it could alternatively be listed as Least Concern (LC).

Discussion. *Emmotum celiae* emerges as a sister species of *E. yapacanum* in the phylogenetic analysis, but the former has smaller leaves (2–5 cm vs. 6–7 cm) with an acute or rounded, slightly mucronate apex (vs. long acuminate).

Additional specimens examined. VENEZUELA. **Amazonas:** alrededor de la laguna Asisa, cerro Asisa, Serranía Parú o Asisa, *J. Hoyos & G. Morillo 88* (CAR, VEN); Serranía Parú, Cerro Parú, just N of valley head of camp, W rim, *R. S. Cowan & J. J. Wurdack 31059* (A, NY); Serranía Parú, Cerro Parú, *R. S. Cowan & J. J. Wurdack 31307* (A, K, NY); valley of Río Coro-Coro, W of Serranía de Yutajé, *B. K. Holst & R. L. Liesner 3273* (A, MO, NY, VEN); valle del Río Coro-Coro, O de la Serranía de Yutajé, *B. K. Holst & R. L. Liesner 3275, 3325* (MO, VEN); 1 a 2 km al E del Río Coro-Coro, O de la Serranía de Yutajé, *R. L. Liesner & B. K. Holst 21480* (A, MO, VEN); Serranía Yutajé, Río Manapiare, lefthand Fork Caño Yutajé, *B. J. Maguire & C. K. Maguire 35275* (MO, NY); Serranía Yutajé, Río Manapiare, Cerro Coro-Coro, *B. J. Maguire & C. K. Maguire 35430* (A, NY); summit of Cerro Parú, Serranía Parú, *K. C. Phelps & H. Hitchcock 513* (A).

4. Emmotum conjunctum R. A. Howard, J. Arnold Arbor. 23(4): 491, tab. 3. 1942. TYPE: Venezuela. Bolívar [Amazonas]: Mt. Auyan-Tepui, 1100 m, Dec.–Jan. 1937–1938, *G. G. H. Tate 1354* (holotype, US!; isotype, NY!). Figure 3.

Shrubs or trees, 2–5 m. *Leaves* coriaceous, sharply bicolored, green-brown or green-grayish on the abaxial surface and dark green on the adaxial surface; lamina 8–12 × 3–7 cm, oblong to narrowly oblong, sometimes elliptic to ovate, apex long acuminate to acute, base rounded or slightly obtuse, sericeous on the abaxial surface, glabrous on the adaxial surface; secondary veins 9 to 13 pairs, conspicuous; petiole (1–)1.2–2 mm. *Inflorescences* axillary, 1- to 5-floriferous branches, up to 4 cm. *Flowers* pentamerous; pedicels to 3 mm; *calyx* campanulate, sepal lobes ca. 1 × 0.8 cm, triangular; *corolla* with the petals white, 5–6.5 × 1.5–2 mm, narrowly oblong, densely pilosulose, forming a beard on the adaxial surface; *stamens* 5–6.5 mm, filaments 4–4.5 mm, slightly swelled; anthers ca. 1 mm, basifixed, connective ovate; *pistil* 4.5–5.5 mm; ovary hirsute; style 3–4 mm, eccentric. *Fruits* ca. 1.5 × 1.5 cm (diam.).

Distribution and ecology. *Emmotum conjunctum* occurs in Venezuela (Amazonas and Bolívar), Guyana, and probably Roraima State in Brazil. It grows in several kinds of savanna or savanna-like associations and forests, always on sandstone-derived substrates, between 300 and 1400 m elevation.

Phenology. *Emmotum conjunctum* flowers year round and fruits between February and November.

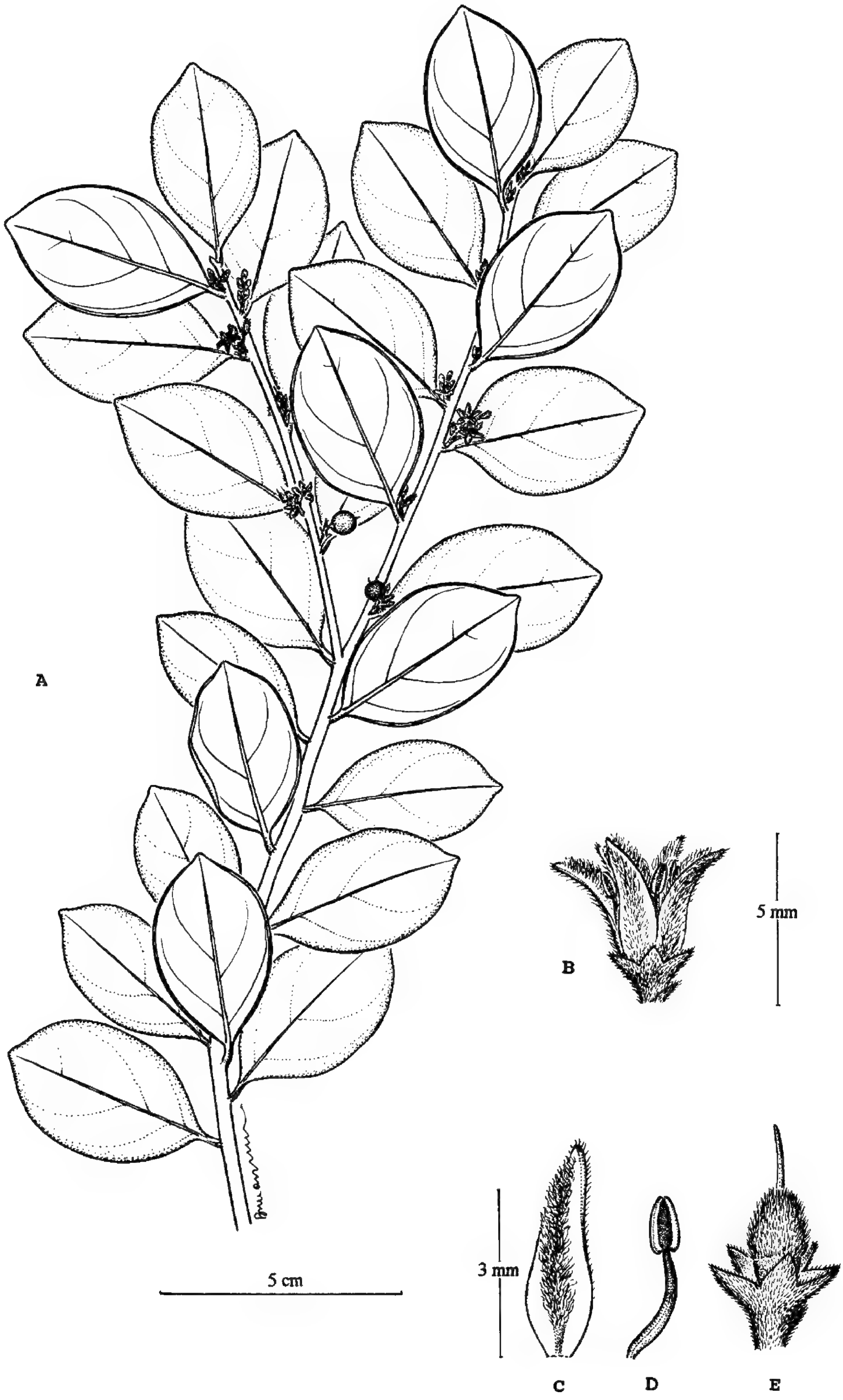

Figure 2. *Emmotum celiae* R. A. Howard. —A. Habit. —B. Flower. —C. Petal inner surface. —D. Stamen. —E. Flower with petals removed and pistil visible. Drawn from *J. Hoyos & G. Morillo 88* (VEN).

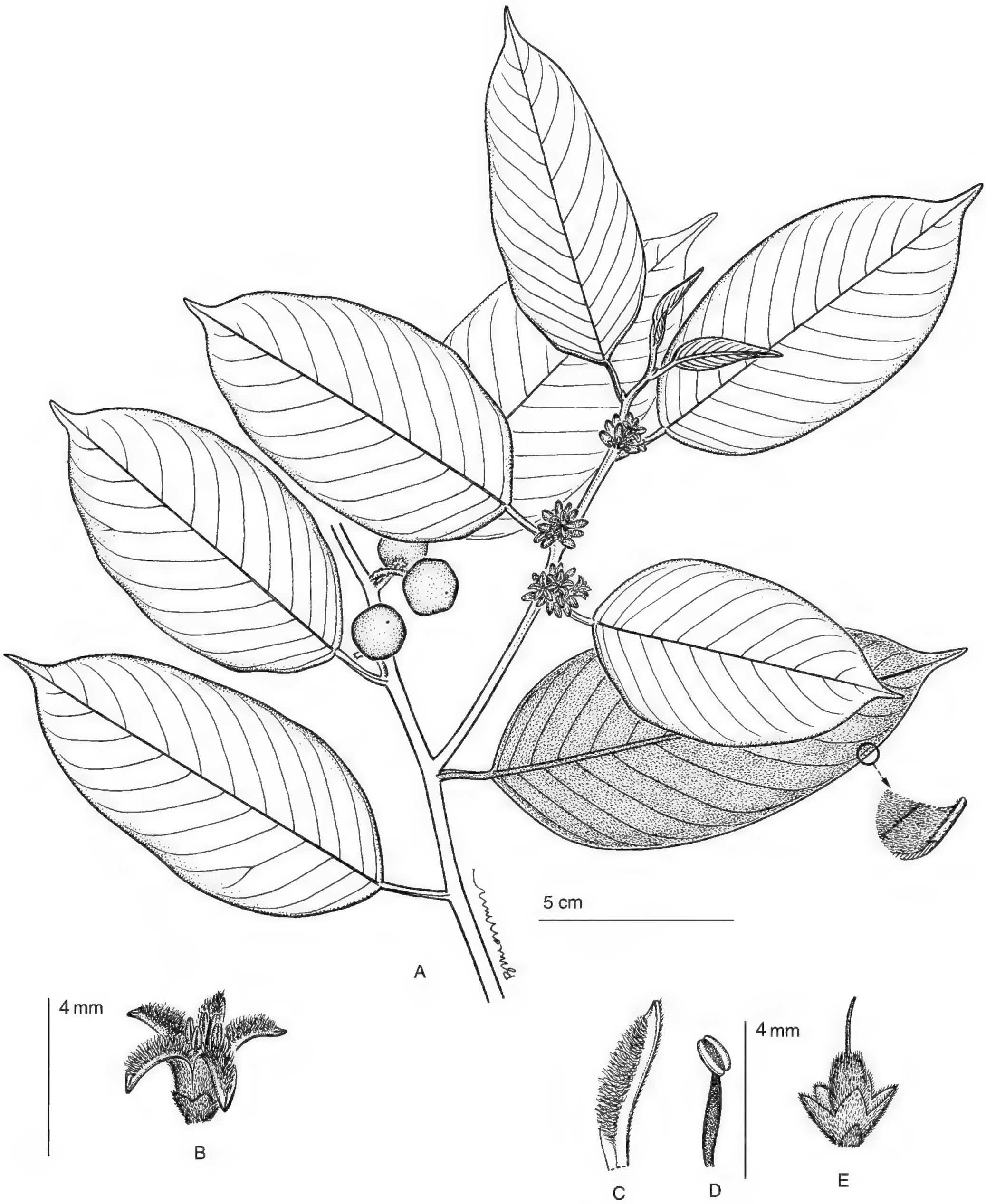

Figure 3. *Emmotum conjunctum* R. A. Howard. —A. Habit. —B. Flower. —C. Petal inner surface. —D. Stamen. —E. Flower with petals removed and pistil visible. Drawn from *Davidse et al. 4898* (VEN).

IUCN Red List category. *Emmotum conjunctum* has a wide distribution, including areas that are protected and that are not densely populated. It is therefore listed as Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Discussion. *Emmotum conjunctum* is sister to *E. fulvum*, but from a phenetic point of view it is also similar to *E. fagifolium*. Both species, *E. conjunctum* and *E. fagifolium*, have been treated in divergent ways by different authors. Howard (1942b) hypothesized a relationship of *E. conjunctum* with *E. fulvum* and *E. affine*. On the other hand, Steyermark (1966) considered it conspecific with *E. fagifolium*, but de Roon (1994) kept both species as separate. The type collections of both species show remarkable differenc-

es, but as more specimens are examined, a close relationship between them becomes evident. However, *E. fagifolium* is limited to the lowlands in the Guianas and Brazil, while *E. conjunctum* is found in the table mountain highlands of Venezuela and Guyana.

Selected specimens examined. VENEZUELA. **Amazonas:** Serranía del Parú (Aroko), *O. Huber 3623, 3628* (A, NY, VEN); Serranía Yutajé, Río Manapiare, left-hand fork Caño Yutajé, *B. J. Maguire & C. K. Maguire 35475* (MO). **Bolívar:** La Gran Sabana, ca. Km 202, S of El Dorado along rd. to Santa Elena, Salto Camá, *G. Davidse et al. 4898* (VEN); O del complejo Guaquinima Tepui, a 42.5 km SE de Entreríos, *G. Aymard & A. Fernández 7126* (MO, NY); Cerro Arepuchi, Río Caroni, *F. Cardona 1938* (NY, VEN); Río Icabarú, Alto Caroni, *F. Cardona 2529* (MO); Gran Sabana along rd. from Icabarú to Santa Elena, 16 km N of Icabarú, *T. B. Croat 54143* (A, MO, NY); cuesta al N de Kamá, *O. Huber et al. 7276* (A, NY, VEN); Río Aza medio en el pie de monte septentrional del cerro Zumbador, *O. Huber 10257* (A, NY, VEN); margen izquierda del Río Trueno alto, aprox. 35 km O del caserio Chiguao, *O. Huber 10331* (A, NY, VEN); en la región del Río Yuruaní inferior, aprox. 5 km al O de San Ignacio de Yuruaní, *O. Huber 10455, 10457* (A, NY, VEN); 3 km S of El Pauji, *R. L. Liesner 19741* (A, MO, VEN); Río Aparamán, affluent of Río Acanán near Yuray-meru rapids, 1.5 km S of SW Amuruay-tepuy, *R. L. Liesner & B. Holst 20115* (A, MO, NY, VEN); faldas meridionales, vecindad de Guayaraca, en la primera (inferior) meseta (hombrillo) arriba del valle de Kamarata, *J. A. Steyermark 94204* (A, NY); Gran Sabana, along valley of Río Kamá, S of Río Kamá, at 199 km S of El Dorado on rd. to Santa Elena, *J. A. Steyermark 111315* (MO, NY, VEN); 8–10 km E de Icabarú, *J. A. Steyermark et al. 117790* (A, MO, VEN); 7 km NO de Icabarú (fl.), *J. A. Steyermark et al. 127311* (MO, VEN); río afluente del Río Uarí, Gran Sabana, *F. Tamayo 3109* (VEN); Mt. Auyan-Tepui, *G. G. H. Tate 1354* (NY [2], US).

5. Emmotum fagifolium Desv. ex Ham., Prodr. Fl. Ind. Occid. (Hamilton) 29. 1825. TYPE: French Guiana, s.d., *N. A. Desvaux s.n.* (holotype, P!).

Pogopetalum acutum Benth., London J. Bot. 2: 377. 1843. TYPE: French Guiana. Cayenne, s.d., *J. Martin s.n.* (holotype, K!; isotypes, G!, P not seen).

Shrubs with decumbent branches or trees, 2–15(–30) m. *Leaves* coriaceous, slightly bicolored, green-brown on the abaxial surface and dark green on the adaxial surface; lamina 6.5–18 × 3–8 cm, ovate to oblong, sometimes elliptic, apex long acuminate to acute, base rounded to slightly obtuse, puberulent on the abaxial surface, glabrous on the adaxial surface; secondary veins 6 to 9 pairs, conspicuous; petiole 1–2 cm. *Inflorescences* axillary, 1- to 5-floriferous branches, up to 4 cm; peduncle short, no longer than 1 cm, *Flowers* pentamerous; pedicels to 3 mm; *calyx* campanulate, sepal lobes ca. 1 × 0.8 cm, triangular; *corolla* with the petals white, 4.5–6 × 1.2–1.5 mm, narrowly oblong, densely pilosulose, forming a beard on the adaxial surface, glabrous on the base; *stamens* 4.5–6 mm, filaments 3.5–4 mm, slightly swelled; anthers ca. 1 mm, basifixed, connective ovate; *pistils* 3.5–4.5 mm, ovary hirsute; style 2.5–3.5 mm, terminal. *Fruits* ca. 1.5 × 1.5 cm (diam.).

Distribution and ecology. *Emmotum fagifolium* ocurrs in Guyana (Barima-Waini, Cuyuni-Mazaruni, Demerara-Mahaica, East Berbice-Corentyne, East Demerara, Essequibo Islands-West Demerara, Mahaica-Berbice, Upper Demerara-Berbice, and West Demerara), Suriname (Nickerie), French Guiana (Cayenne), and Brazil (Acre, Amapá, Amazonas, Maranhão, Pará, and Pernambuco). It grows in shrublands, riparian forests, and savanna with trees in sandy soil, between 100 and 300 m elevation.

Phenology. *Emmotum fagifolium* flowers year round and fruits from December to March.

IUCN Red List category. There are many collections of this species occurring over a large area, including areas that are protected and that are not densely populated. It is therefore listed as Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Vernacular names and uses. Bois de'Agouti, harriromanabading, muirachimbé, muira-ximbé, pao de ramo (Howard, 1942b). De Roon (1994) included the following names: candlewood, manobodin, harrar-iro-manobodin (Guyana), and bois d'agouti (French Guyana). Corrêa (1984) mentioned that the wood is excellent for fire. Its local names in Brazil are muirachimbé and marachaimbé.

Discussion. In the phylogenetic analysis, *Emmotum fagifolium* is resolved as sister species to a clade including *E. glabrum*, *E. celiae*, and *E. yapacanum*. From a phenetic standpoint, however, it is also similar to *E. affine* and *E. conjunctum*. It has ovate to oblong, sometimes elliptic leaves (vs. elliptic to ovate in *E. affine* and oblong to narrowly oblong in *E. conjunctum*) that are puberulent on the abaxial surface (vs. sericeous). The sister clade (*E. glabrum*, *E. celiae*, and *E. yapacanum*) features smaller leaves with fewer, less conspicuous secondary veins, and shorter petioles.

Additional specimens examined. BRAZIL. **Acre:** estr. Isac, aprox. 4 km da cidade, *C. A. Cid Ferreira et al. 10942* (A). **Amapá:** BR 156, betw. Calçoene & Rio Amapá Grande, 30 km S of Calçoene, *S. Mori & R. Cardoso 17360* (A, NY). **Amazonas:** Rio Jarí, Monte Dourado, Planalto A, *N. T. Silva 1006* (A, NY [2]). **Pará**: Belem, Catú, *A. Ducke 1616* (A, F, MG, NY, R); Turiaçu, Km 6 de BR 106, Maracaçuma–Sta. Elens, *N. A. Rosa & H. Vilar 2794* (F,

GH, NY); margem da estr. Gurupá, Rio Tajapuri, Km 4, *N. T. Silva & C. Rosario 5092* (F, GH, NY); alto de Alegria, *E. H. Snethlage 341* (F). **Pernambuco:** Madeiros Costa Cabo, area proj. Suape, *A. Lima 22267* (F). FRENCH GUIANA. **Cayenne:** Isle de Cayenne, *J. J. Granville 9122* (NY, US); Cayenne, *Martin s.n.* (F [photo], GH, K, US [photo]); near rd. (Hwy. D5) from Tonate to Montsinery & Tonnegrande, *L. Skog et al. 7028* (B, F, G, K, M, NY, US). GUYANA. **Barina-Waini:** Barima River, *J. S. de la Cruz 3375* (GH, NY). **Cuyuni-Mazaruni:** Kuroba, E on Mazaruni River, 3 km N of confluence of Kamarang River with Mazaruni River, *D. Clarke 806* (MO, US); Arabapo, Mt. Roraima, *Forest Department 2829* (K); Pakaraima Mtns., Kako Ameridian village, Kako River, *P. J. M. Maas & L. Y. Th. Westra 4364* (K); Mazaruni Station, *N. Y. Sandwith 1547* (B, M, NY). **Demerara-Mahaica:** Soesdyke-Linden Hwy., 2–3 km SW of Timehri airport at jct. of minor rd., *L. J. Gillespie 2653* (MA, NY); Imbaimadai, Partang River crossing, 1 km from mouth, *L. J. Gillespie & D. R. Smart 2679* (CTES, NY); Demerara River, *Jenman 4868* (K); Linden-Soesdyke Hwy., betw. Dora & Maibia Creek, *J. J. Pipoly et al. 9714* (NY); Yarrowkabra settlement & Forestry Station E & W of Timehri-Linden Hwy., *J. J. Pipoly & H. Godfrey 7462* (F, NY, US). **East Berbice-Corentyne:** lt. (S) bank upper Canje River W of Digitima Creek, *J. J. Pipoly et al. 9441* (NY). **Essequibo Islands-West Demerara:** near Bartica, green heart Wallaba forest, *T. A. W. Davis 1009* (K); Mabura region, Centra, CD 920 rd., *R. C. Ek 743* (NY); Mabura Hill, 180 km SSE of Georgetown, Mabura main rd., *H. ter Steege & P. del Jager 400* (B, M, US); W border of Atkinson Field, *H. S. Irwin 199* (US). **Mahaica-Berbice:** 4 km from Santa Misión, *A. R. A. Gorts-van Rijn 401* (K). **Upper Demerara-Berbice:** Mackenzie Mines area, vic. E of Utuni, 35 mi. S of Mackenzie, *R. S. Cowan 39241* (A, NY); 10 km S of Soesdyke on rd. to Linden, behind forest station & along creek, *W. Hahn & S. Tiwari 4789* (CTES, NY); Atkinson Field Army Barracks, E Bank Demerara, *S. A. Harris 49* (K); from trail near Camp 18 on R. B. Kurudimi, River Demerara, *L. S. Honenkerk 131a* (K); Sand Hill, 35 mi. up Demerara River, *B. R. Wood 893* (K). SURINAME. **Nickerie:** area of Kabalebo Dam Project, *N. M. Heyde & J. C. Lindeman 240* (K).

6. Emmotum floribundum R. A. Howard, J. Arnold Arbor. 23(4): 487, tab. 2. 1942. TYPE: Peru. Loreto: Mishuyacu, near Iquitos, 100 m, forest, Apr. 1930, *A. Klug 1212* (holotype, F!; isotype, US!).

Shrubs or tree, to 10 m. *Leaves* coriaceous, sharply bicolored, green-brown on the abaxial surface and dark green and shiny on the abaxial surface; lamina 8–14 × 4–8 cm, ovate, elliptic, or oblong, sericeous on the abaxial surface, glabrous on the adaxial surface, apex acute or mucronate, base rounded to slightly obtuse; secondary veins 8 to 11 pairs, conspicuous; petiole 1.5–2.5 cm. *Inflorescences* axillary, sometimes cauliflorous, 1- to 3-floriferous branches, up to 4 cm; peduncle short, no longer than 1 cm. *Flowers* pentamerous; *calyx* campanulate, sepal lobes ca. 1 × 0.8 cm, triangular; *corolla* with petals white, 5.5–6 × 1.2–1.5 mm, narrowly oblong, densely pilosulose, forming a beard on the adaxial surface; *stamens* 5.5–6 mm, filaments 4.5–5 mm, slightly swelled; anthers ca. 1.2 mm, dorsifixed, connective ovate; *pistils* 5–5.5 mm, ovary hirsute; style 3.5–4 mm, centric. *Fruit* ca. 1.5 × 1.5 cm (diam.).

Distribution and ecology. *Emmotum floribundum* ocurrs in Colombia (Amazonas, Caquetá, and Vaupés), Venezuela (Amazonas), Guyana, Peru (Loreto), and Brazil (Acre and Amazonas). It grows in riparian forest that is susceptible to flooding and in shrubland between 80 and 150 m elevation.

Phenology. *Emmotum floribundum* flowers from November to August and fruits from October to July.

IUCN Red List category. The few known collections of this species are scattered over a large area, including areas that are protected and that are not densely populated. It is therefore listed as Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Vernacular names and uses. In Peru it is known as ingaina (Howard, 1942b) and in Venezuela as yurí de caracol.

Discussion. According to our analysis, *Emmotum floribundum* is the sister species of *E. acuminatum*. Both species have dorsifixed anthers and a glabrous ovary with a long eccentric style. It differs from *E. acuminatum* in its ovate, elliptic, or oblong lamina (vs. oblong to ovate, rarely elliptic) that is sericeous on the abaxial surface (vs. puberulent) and with eight to 11 pairs of secondary veins (vs. six to nine pairs).

Additional specimens examined. BRAZIL. **Acre:** Mâncio Lima, Ramal do Banho, 5 km NW of Mâncio Lima, *D. C. Daly et al. 9050* (NY). COLOMBIA. **Caquetá:** Región Araracuara, *D. Restrepo & A. Matapi 443* (F, MO). **Vaupés:** Río Apaporís, Raudal Yayacopi (la playa) & vic., *R. E. Schultes & I. Cabrera 15504* (NY). GUYANA. **Cuyuni-Mazaruni:** mouth of Kako River (upper Mazaruni tributary), *A. S. Pinkus 193* (MO). PERU. **Loreto:** Quebrada Shushuma near rd. to Mapa Cocha, ca. 17 km from Iquitos, *S. MacDaniel & M. Y. Rimachi 22469* (F); carr. Zungaro Cocha, cerca de quebrada Shushuma, *M. Y. Rimachi 6531* (F, NY, US). VENEZUELA. **Amazonas:** Río Sipapo, 4–5 km arriba de la boca del Río Guyapo, ca. la población piaroa de San Felipe (Raudalito), *G. Carnevali et al. 1700* (MO); San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro & Brazo Casiquiare, *H. L. Clark & P. Maquirino 8078* (MO, NY); San Carlos de Río Negro, 20 km de la confluencia del Río Negro y Brazo Casiquaire, *F. Delascio et al. 9625* (VEN); Río Baría, *A. Gentry & B. Stein 47359* (A, MO, NY, VEN); Caño Caname, afluente derecho (oriental) del medio Río Atabapo, sabana de Cucurital, 20 km E de la boca, *O. Huber et al. 3730* (A, NY, VEN);

sabana ubicada a unos 10 km S del Río Autana y unos 15 km al SW del Cerro Autana, *O. Huber et al. 4053* (A, NY [2]); Sabana Morocoto just W of Cerro Morocoto, below San Fernando de Atabapo, *J. S. L. Level 16* (A, NY, VEN); N de Raudalito, Río Sipapo, *G. Romero & F. Guánchez 1627* (GH, NY, VEN); Santa Rosa de Ucata, *G. Romero & F. Guánchez 1862* (GH, MO, NY); base del Cerro de la Neblina, Río Baría, from the Río Mawarinuma, *W. W. Thomas et al. 3464* (F, MO, NY, VEN); in Sabanita Morocoto (rt. bank 2 km below mouth of Atabapo), *J. J. Wurdack & L. S. Adderley 42696* (GH, NY, VEN).

7. Emmotum fulvum R. A. Howard, J. Arnold Arbor. 23(4): 493, tab. 4. 1942. TYPE: Venezuela. Bolívar [Amazonas]: Arabupu, vic. of Mt. Roraima, 4200 ft., 21 Dec. 1938, *Pinkus 87* (holotype, NY!; isotypes, BR not seen, F!, U not seen, US!).

Shrubs or tree, to 30 m. *Leaves* coriaceous, sharply bicolored, brown ferruginous to golden on the abaxial surface, dark green and shiny on the adaxial surface; lamina 10–16 × 4–6 cm, ovate to narrowly ovate, velvety on the abaxial surface, glabrous on the adaxial surface, apex narrowly acute, base rounded or slightly obtuse; secondary veins 6 to 9 pairs; petiole ca. 1.5 cm. *Inflorescences* axillary, sometimes cauliflorous, 1-to 3-floriferous branches, up to 2 cm; peduncle short, no longer than 1.5 cm. *Flower* pentamerous; pedicels up to 3 mm; *calyx* campanulate, sepal lobes ca. 1 × 0.8 cm, triangular; *corolla* with petals white, 5.5–6 × 1–1.2 mm, narrowly oblong, densely pilosulose, forming a barbed indument on the adaxial surface; *stamens* 5–5.5 mm, filaments 4.5–5 mm, slightly swelled; anthers 1–1.2 mm, basifixed, connective ovate; *pistils* 5–5.5 mm, ovary hirsute; style 3–3.5 mm, centric. *Fruits* ca. 1.5 × 1.5 cm (diam.).

Distribution and ecology. *Emmotum fulvum* is endemic to Venezuela, where it has been collected in the state of Bolívar. It is possibly found in Guyana (de Roon, 1994). It grows in low, medium to tall forests on tepui slopes, between 850 and 1700 m elevation.

Phenology. *Emmotum fulvum* flowers from November to May.

IUCN Red List category. The few known collections of this species are scattered over a large area, including several areas that are protected and that are not densely populated. It is therefore listed as Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Vernacular names and uses. In Venezuela it is know as apory-ban-yek (Pemón).

Discussion. According to the phylogenetic analysis, *Emmotum fulvum* is the sister species of *E. conjunctum*, but the former has a narrowly ovate lamina with a dense velvety indument on the abaxial surface with long hairs (vs. oblong to narrowly oblong and sericeous on the abaxial surface).

Additional specimens examined. VENEZUELA. **Bolívar:** vic. of Arapubu [Arobopo], *A. P. Pinkus 87* (GH, NY [2]); Cerro Uei, entre Luepa y Cerro Venamo, *J. A. Steyermark & Nilsson 466* (A, NY, VEN); Macizo de Chimantá, Amurí-tepui, *J. A. Steyermark & J. J. Wurdack 1367* (A, VEN); Ptari-tepui, *J. A. Steyermark 60671* (A, NY, VEN); Macizo de Chimantá, *J. A. Steyermark 75141* (NY, VEN); SW face of Chimanta-tepui (Torono-tepui), above Río Tirica, *J. A. Steyermark 75430* (G, NY [2]); Cerro Venamo, *J. A. Steyermark et al. 92715* (A, F, NY, VEN).

8. Emmotum glabrum Benth. ex Miers, Ann. Mag. Nat. Hist., ser. 3, 4: 366. 1859. TYPE: Venezuela. Amazonas: Rio Guainia & Rio Casiquiare in Brasilia Septentrionali, *R. Spruce 3536* (lectotype, designated by de Roon [1994: 98], K! [specimen on blue card]; isotypes, G!, K!, MO!, NY!, P not seen). Figure 4.

Emmotum argenteum Gleason, Bull. Torrey Bot. Club 58: 386. 1931. TYPE: Venezuela. Amazonas: Mt. Duida, on slopes at Central camp, 4800 ft., [*G. H. H. Tate*] *564* (holotype, NY!).

Emmotum ptarianum Steyerm., Fieldiana, Bot. 28(2): 341. 1952. TYPE: Venezuela. Bolívar: collected in vic. of "Misia Kathy Camp," SE-facing slopes, Ptari-tepuí, 1585–1600 m, 10–11 Nov. 1944, *J. A. Steyermark 59974* (holotype, F!; isotypes, MO not seen, NY!, P not seen, US!, VEN!).

Shrubs to trees, to 20 m. *Leaves* subcoriaceous, nonbicolored, dark green or brown on both surfaces; lamina 5–13 × 3–6 cm, elliptic to oblong, sometimes ovate, puberulent on the abaxial surface, with few, long, white, and adpressed hairs, especially along the main nerve, glabrous on the adaxial surface, apex long acuminate, up to 2 cm, sometimes acute, base slightly obtuse or slightly attenuate; secondary veins 2 to 5 pairs, inconspicuous; petiole 0.5–0.8(–1) cm. *Inflorescences* axillary, sometimes cauliflorous, 1-floriferous branches, up to 2 cm, peduncle short, no longer than 1.5 cm. *Flowers* pentamerous; *calyx* campanulate, sepal lobes ca. 1 × 0.8 cm, triangular; *corolla* with petals white, 3.5–4 × ca. 1 mm, narrowly oblong, densely pilosulose, forming a beard on the adaxial surface; *stamens* 3–4 mm, filaments 2.8–3 mm, slightly swelled; anthers 1–1.2 mm, basifixed, connective ovate; *pistil* 4–4.5 mm, ovary hirsute; style 2.5–3 mm, centric. *Fruits* ca. 1.5 × 1.5 cm (diam.).

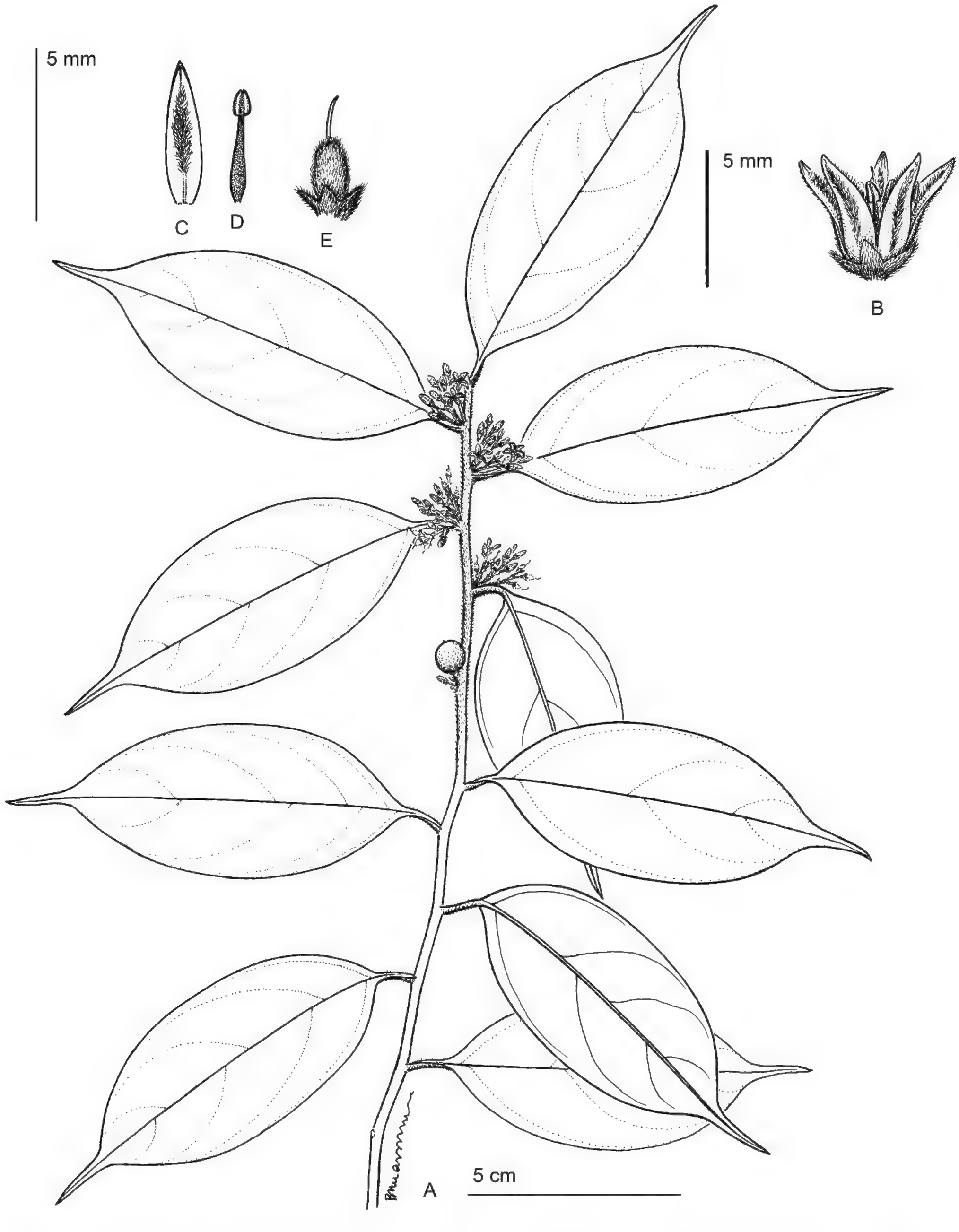

Figure 4. *Emmotum glabrum* Benth. ex Miers. —A. Habit. —B. Flower. —C. Petal inner surface. —D. Stamen. —E. Flower with petals removed and pistil visible. Drawn from *J. A. Steyermark & B. K. Holst 130635* (VEN).

Distribution and ecology. *Emmotum glabrum* ocurrs in Colombia (Vaupés), Venezuela (Amazonas and Bolívar), Guyana (Potaro-Siparuni and Cuyuni-Mazaruni), Peru (San Martín), and Brazil (Amazonas). The collection from Peru represents a clear disjunction in the distribution of this species; the collection from Brazil is very near the Venezuelan frontier. It grows in riparian forest, montane forests, shrubland, tepui meadows, and open rocks on sandstones, between 100 and 1800 m elevation.

Phenology. *Emmotum glabrum* flowers and fruits from October to May.

IUCN Red List category. There are many known collections of this species scattered over a large area, including protected areas and areas that are not densely populated, and it is therefore listed as Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Discussion. In the phylogenetic analysis, *Emmotum glabrum* is the sister species of a clade including two species, *E. celiae* and *E. yapacanum*. *Emmotum glabrum* differs from *E. celiae* by the larger lamina (5–13 cm vs. 2–5 cm), the acuminate apex (vs. acute to slightly mucronate), and the number of secondary veins (two to five vs. two to three pairs); it differs from *E. yapacanum* by its shorter peduncle (less than 1.5 cm vs. 4 cm).

Emmotum glabrum has been registered three times in Brazil (Engler, 1872; Carvalho et al., 1973; Prance & Johnson, 1992), but the collections mentioned in the first two publications belong to *E. nitens* and *E. amazonicum*, respectively. Only the collections from Serra do Aracá, very near the Venezuelan border, belong to *E. glabrum* (Prance & Johnson, 1992).

Emmotum glabrum was originally described by George Bentham in 1859 from the collection *Richard Spruce 3536* from Amazon State (Venezuela) as type. Two sheets from the personal herbarium of Bentham were deposited at Kew and neither was annotated by him as type material. These two specimens were studied by A. C. de Roon in 1993 and labeled as holotype (collection with the flowers mounted on the blue card) and isotype, respectively. One year later, he published the treatment of the family for the *Flora of the Guianas* (de Roon, 1994), citing *R. Spruce 3536* as the holotype. In doing so, he de facto lectotypified the name with that specimen.

Additional specimens examined. BRAZIL. **Amazonas:** Serra da Aracá, parte SE da Serra Norte, *Amaral do. I. L. 1603* (MO, NY); Margenes do R. da Serra Aracá, *M. A. Rosa & S. B. Lira 2313* (A, NY); Serra da Aracá, parte SE da Serra Norte, *A. S. Tavares & M. G. Silva 51* (NY); Serra da Aracá, parte SE da Serra Norte, *A. S. Tavares & M. G. Silva 82* (NY). COLOMBIA. **Guainía:** Maimachi, Serranía del naquén, Cerro Minas, alrededores del Helipuerto 15 y camino hasta la cima del cerro, *C. Barbosa & S. Madriñan 8362* (MO). GUYANA. **Cuyuni-Mazaruni:** Mazaruni-Potaro Region, Upper Mazaruni River Basin, Pakaraima Mtns. Peak, N of Karowrieng Rivers, *J. J. Pipoly & K. Alfred 7717* (B, F, GH, M, MO, NY, US); Upper Mazaruni River Basin, SE ridge of Merume Mtns., *S. S. Tillet et al. 44832* (A, F, K, NY). **Potaro-Siparuni:** Kaieteur savannah, Potaro Rivers, *G. S. Jenman 1050* (K); Kaieteur plateau, *B. J. Maguire & B. Fanshane 23339* (A, F, K, MO, NY, VEN). PERU. **San Martín:** Chazuta, Río Huallaga, *G. Klug 3990* (F, GH, K, NY, US). VENEZUELA. **Amazonas:** Región Duida Marahuaca, *V. Barnes 35* (VEN); Cerro Aracamuni, *G. Carnevali et al. 2583* (VEN); laderas SE del Cerro Huachamacari, *F. Delascio 12356* (VEN); slope of Cerro de Marahuaca, *R. L. Liesner 17738* (MO, NY); on plateau of Duida above Culebra, *R. L. Liesner 18182* (MO, NY); slope of Huachamacari, *R. L. Liesner 18342* (MO, NY, VEN); Cerro Aracamuni, *R. L. Liesner & G. Carnevali 22670* (A, MO, NY); Cerro Marahuaca, Sima area, *R. L. Liesner 25057* (A, NY); Cerro Sipapo (Paráque), below escarpment at camp, *B. J. Maguire & L. Politi 27562* (GH, NY); Cerro Duida, *B. J. Maguire & B. Maguire, Jr. 29165* (GH, NY, VEN); Río Guianía, just S of Maroa, *B. J. Maguire 36447* (A [2], COL, NY [2]); Cerro de la Neblina, on Cañón Grande slopes E of Cumbre Camp, *B. J. Maguire et al. 42177* (A, NY); Cerro de la Neblina, Río Yatua, Cañón Grande, *B. J. Maguire et al. 42230* (A, NY, VEN); Guainía entre el Río Negro y el Casiquiare, *R. Spruce 3536* (BM, F, G, GH, K, MO [photo], NY, US [photo]); faldas del extremo N del Cerro Duida, al SO de la comunidad de Culebra, *J. A. Steyermark et al. 126138* (A, NY, VEN); Pimichín, Guainía, *L. L. William 14946* (A, VEN). **Bolívar:** base central del Guaquinima-tepui, quebrada Martínez, *G. Aymard C. 5985* (MO, VEN); Cerro Guaquinima, camp 4, *B. Boom 9370* (A); Amaruay-tepuy, *B. K. Holst & R. L. Liesner 2828* (A, MO, VEN); Piar, Río Acanan, Guaruma, 5 km SW by air of confluence with Río Carrao, E of Auyan-tepui, *B. K. Holst & R. L. Liesner 2855* (A, MO, NY); Uaiparú, 50 km al NNW de Icabarú, *O. Huber & A. Fernández 11328* (NY, VEN); Cerro Venamo, a lo largo del afluente derecho (O) subiendo el Río Venamo, descendiendo el río desde el campamento, *J. A. Steyermark et al. 92366* (A, NY, VEN); Cerro Marutaní, NNW of camp 2 along tributary of Río Carla, *J. A. Steyermark et al. 124070* (MO, NY, VEN); Cerro Marahuaca, *J. A. Steyermark & B. Holst 130635* (A, MO); Chimantá, vic. camp 3, beside small stream, lower slopes of Tirepón-tepui, *J. J. Wurdack 34043* (A, NY, VEN); middle slopes of Sarvén tepuí, *J. J. Wurdack 34100* (A, NY).

9. Emmotum yapacanum R. A. Howard, Mem. New York Bot. Gard. 29: 66, fig. 56. 1978. TYPE: Venezuela. Amazonas: Cerro Yapacana, *B. Maguire, R. S. Cowan & J. J. Maguire 30518* (holotype, NY!; isotype, A!). Figure 5.

Shrub or trees, to 3 m. *Leaves* subcoriaceous, nonbicolored, dark brown on both surfaces; lamina 6–7 × 2.8–3.2 cm, elliptic, pubescent on the abaxial surface, glabrescent, apex long acuminate, to 2.5 cm, sometimes acute; secondary veins 2 to 3 pairs, inconspicuous; petioles 0.5–0.8 cm. *Inflorescences* axillary, sometimes cauliflorous, 1-floriferous branches, to 4 cm; peduncle ca. 4 cm. *Flowers* pentamerous; *calyx* campanulate, sepal lobes ca. 1 × 0.7 mm, triangular; *corolla* with petals 4.5–5 × ca. 1 mm, narrowly oblong, densely pilosulose, forming a beard on the adaxial surface; *stamens* 3.5–4 mm, filament 2.5–4 mm, slightly swelled; anthers 1–1.2 mm, basifixed, connective ovate; *pistils* 4–4.5 mm, ovary hirsute; style 2.5–3 mm, centric. *Fruits* ca. 1.5 × 1.5 cm (diam.).

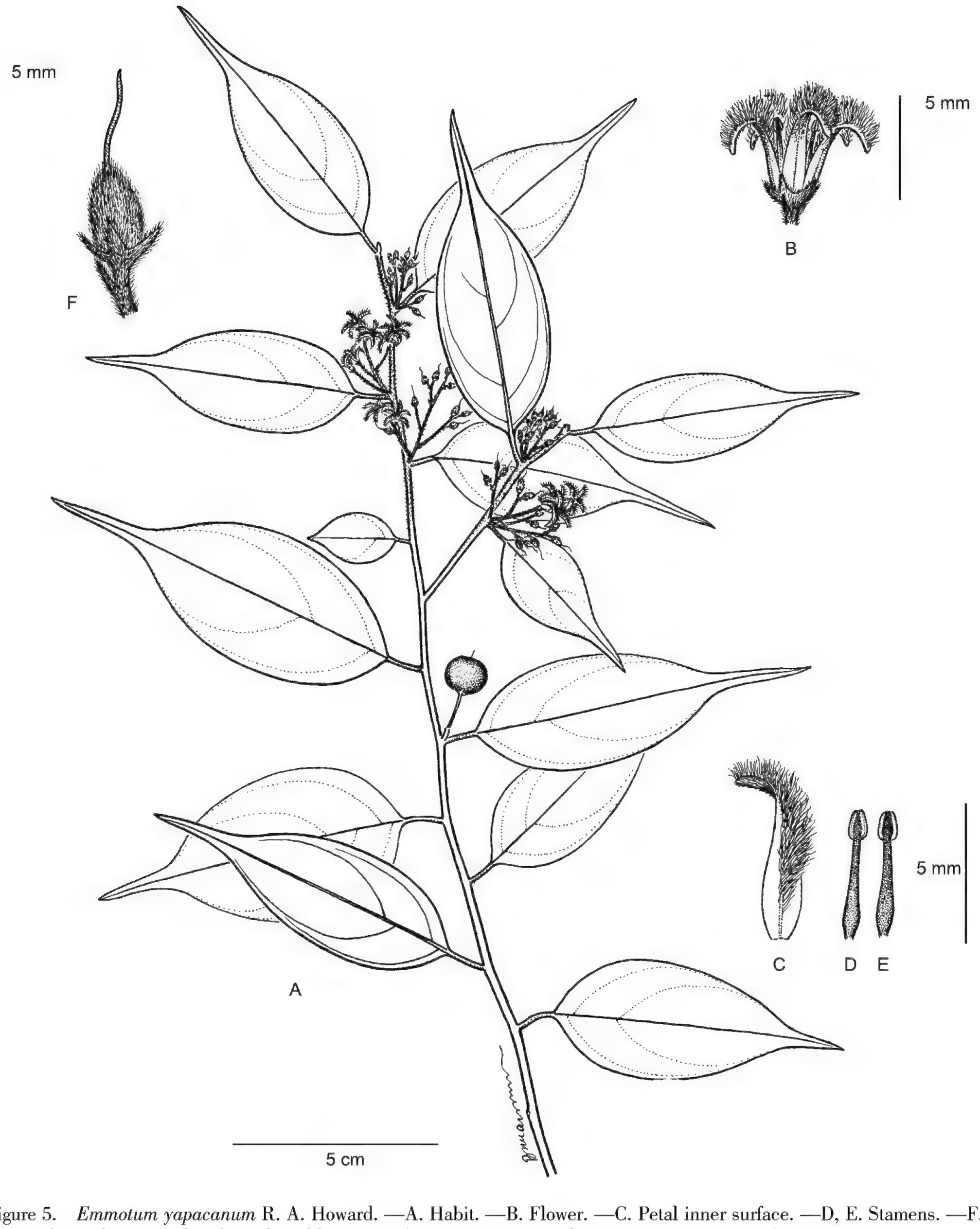

Figure 5. *Emmotum yapacanum* R. A. Howard. —A. Habit. —B. Flower. —C. Petal inner surface. —D, E. Stamens. —F. Flower with petals removed and pistil visible. Drawn from *J. A. Steyermark & G. Bunting 103139* (VEN).

Distribution and ecology. *Emmotum yapacanum* is endemic to Venezuela. It has only been collected in Amazonas State. It grows on shrublands on sandstone-derived substrates between 800 and 1300 m elevation.

Phenology. *Emmotum yapacanum* flowers between January and March.

IUCN Red List category. *Emmotum yapacanum* is only known from three collections. It could be best listed as Data Deficient (DD). However, because it is restricted to isolated sandstone table mountain slopes and summits in a completely inaccessible area, it could alternatively be listed at Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Discussion. *Emmotum yapacanum* is the sister species of *E. celiae* in the phylogenetic analysis. From a phenetic point of view it is very similar to *E. glabrum*, from which it differs by its longer peduncle (ca. 3 cm vs. ca. 1.5 cm long). It is possible that *E. yapacanum* represents an extreme variation of *E. glabrum* with a long peduncle. However, more material from the type locality in the Cerro Yapacana is necessary.

Additional specimens examined. VENEZUELA. **Amazonas:** NW slopes of Yapacana, *B. Maguire et al. 30518* (NY); cumbre del Cerro Yapacana, *J. S. Steyermark & G. Bunting 103139* (A, MO, NY, VEN).

Ib. Emmotum sect. **Brevistyla** Engl., Fl. Bras. (Martius) 12(2): 44. 1872. TYPE: *Emmotum nitens* (Benth.) Miers [≡ *Pogopetalum nitens* Benth.], s.d., *C. A. Gardner 3309* (lectotype, designated by Duno et al. [2007: 308], K!).

Pogopetalum Benth., Proc. Linn. Soc. London 1(10): 87–88. [6 Apr.] 1841. TYPE: *Pogopetalum orbiculatum* Benth. [≡ *Emmotum orbiculatum* (Benth.) Miers] (lectotype, designated here).

This section is characterized by flowers with the petals lanate within, but with only two clusters at the base and the apex, rarely these trichomes are laxly continuous along the inner surface of the petal; filaments that are dilated both at the base and the apex; anthers that are oblong, with the connective elliptic in shape and prolongated at the apex; the ovary distinguished by the short style, less than 0.5 mm long; and by the absence of eccentric styles. This section includes *Emmotum amazonicum*, *E. harleyi*, *E. nitens*, and *E. orbiculatum*.

1. Emmotum amazonicum Duno & Carnevali, sp. nov. TYPE: Brazil. Amazonas: Manaus, Rio Tarumá, silva inundabilis, 27 Oct. 1943 (fl.), *A. Ducke 1413* (holotype, NY!; isotypes, GM not seen, IAN not seen, US!).

Species *Emmoto nitenti* (Benth.) Miers affinis, sed ab eo foliis concoloribus abaxialiter puberulis (vs. dense pubescentibus), nervis secundariis 11 ad 14 et ovario glabro differt.

Shrubs or tree, up to 12 m high. *Branches* cylindrical, sulcate, covered by fine tomentum. Leaves exstipulate, coriaceous, sulcate, puberulent, not bicolored, dark brown on both surfaces; lamina 7–10 × 3–5 cm, elliptic to elliptic-oblong, adaxial surface glabrous, abaxial surface brown-yellow puberulent, apex acute, base rounded, margin entire, slightly revolute; secondary veins 11 to 14 pairs, 3–5 mm between them; petiole 1–1.5 cm. *Inflorescence* axillary, a short panicle, flower pentamerous, hermaphroditic; bract triangular, ca. 1 × 1 mm, adaxial surface glabrous, abaxial surface sericeous-tomentose; pedicel articulate; *calyx* campanulate, sepal lobes ca. 0.5 × 0.5 mm, triangular, concave, with the apex acute, adaxial surface glabrous, abaxial surface tomentose; *corolla* with petals reflexed when mature, ca. 2.6 × 1 mm, adaxial surface sericeous-tomentose, abaxial surface with 2 tufts of hair at the base and apex; apex acute, with a diminute end on the adaxial surface; *stamens* incurved, filaments ca. 2 mm, slightly thickened with a dilated apex, connective elliptic, apex slighty prolongated; anthers basifixed, cordate, ca. 1.5 mm; *pistils* with the ovary globose, glabrous, style short and curved at the apex, ca. 0.5 mm long, stigma obsolete, diminute 3-lobate. *Fruit* a drupe, subglobose, ca. 1.5 × 2.4–2.5 cm (diam.), unilocular, sometimes with the crest not very well developed; seed solitary.

Distribution and ecology. *Emmotum amazonicum* is endemic to Brazil, where it is only known from the states of Amazonas; there it grows in forest between 0 and 100 m elevation.

Phenology. *Emmotum amazonicum* has been collected in flower in October and fruit in January.

IUCN Red List category. Because this species is only known from three collections, it is listed as Data Deficient (DD) according to IUCN Red List criteria (IUCN, 2001).

Discussion. In the current phylogenetic analysis, *Emmotum amazonicum* is the sister species of a clade that includes three taxa: *E. harleyi*, *E. nitens*, and *E. orbiculatum*. From a strictly phenetic point of view, however, it is most similar to *E. nitens*. *Emmotum amazonicum* differs from *E. nitens* in the lamina that is not strongly bicolored and with a dense indument on the abaxial surface, the number of secondary veins (11 to 14 vs. six to eight pairs), and the glabrous ovary. Furthermore, this taxon is known to occur only in the Brazilian Amazon Basin (Amazonas), to the north of the distribution of *E. nitens*, which occurs in the southern part of Amazonas, and from Bahia, Distrito Federal, Goiás, Maranhão, Mato Grosso, Minas Gerais, Pará, and Pernambuco, as well as Bolivia (Beni, La Paz, and Santa Cruz).

Paratypes. BRAZIL. **Amazonas:** 20 km NW of Manaus, *B. W. Nelson & S. P. Nelson 1045* (NY); Reserva Florestal Ducke, Manaus–Itacoatiara, Km 26, *J. M. Brito & P. A. C. L. Assunção 40* (K, MO); Reserva Florestal Ducke, Manaus–Itacoatiara, Km 26, *A. Vicentini 828* (K, MO, NY).

2. Emmotum harleyi Duno, Novon 17(3): 306–308, fig. 1. 2007. TYPE: Brazil. Bahia: 19.5 km SE of Morro do Chapeu on BA052, rd. to Mundo Novo, by Rio Ferro Doido, ca. 900 m, ca. 11°38′S, 41°02′W, 2 Mar. 1977 (fl.), *R. M. Harley, S. J. Mayo, R. M. Storr, T. S. Santos & R. S. Pinheiro 19248* (holotype, K!; isotypes, K!, NY!). Figure 6.

Shrubs to small trees, to 5 m. *Leaves* coriaceous, sharply bicolored, dark green and shiny adaxially, yellow or golden abaxially; lamina 5–10 × 3–4.5 cm, elliptic or widely elliptic, rarely ovate or narrowly ovate, apex acute, rarely acuminate, attenuate, shortly acuminate, or emarginate, base rounded, margin entire, slightly revolute; secondary veins 9 to 11 pairs, well developed but hidden by a dense indument; adaxially glabrous, abaxially densely tomentose with crisped hairs ca. 0.2 mm long; petioles 1.3–1.5 cm. *Inflorescences* axillary, 1- to 4-floriferous branches per axil. *Flowers* pentamerous; *calyx* campanulate, sepal lobes, ca. 1 × 0.8 mm, triangular; *corolla* with white petals, 2.5–3 × ca. 1 mm, ovate or narrowly ovate, slightly bearded on the inner surface; *stamens* 2.5–3 mm, filament 1.5–1.8 mm, basally dilated; anthers basifixed, connective elliptic, slightly prolongated at the apex; *pistils* with the ovary glabrous; style terminal, very short, no longer than 0.5 mm. *Fruit* 1–1.2 × 1–1.5 cm (diam.).

Distribution and ecology. *Emmotum harleyi* is endemic to Brazil, where it is only known from the Chapada Diamantina including the Serra do Tombador in Bahia. It grows mainly in campo rupestre over white crystalline sand rock, between 800 and 1200(1450) m elevation, and more rarely on mata ciliar at 500 m.

Phenology. *Emmotum harleyi* flowers from September to July and fruits from September to June.

IUCN Red List category. The information about the population status of this species is far from complete to produce a precise conservation evaluation, but some general information can be gathered from specimen labels. *Emmotum harleyi* occurs along discontinuous patches in an area of ca. 100,000 km^2. There are numerous botanical collections, including some made inside protected areas such as Parque Municipal de Mucugê, Parque Municipal Natural da Serra das Almas, Parque Nacional da Chapada Diamantina, and Santuario Ecologico do Largo do Queiroz, among others. Despite the fact that the cerrado and campo rupestre are two of the most threatened ecosystems in northeastern Brazil, the populations of this species seem to be large enough to be excluded from any category of protection according to IUCN Red List criteria (IUCN, 2001) or listed as Least Concern (LC).

Vernacular name. Aderno.

Discussion. In the phylogenetic reconstruction, *Emmotum harleyi* is the sister species of a clade with two species, *E. orbiculatum* and *E. nitens*. However, from a phenetic point of view it is more similar to *E. nitens* because in both species the filament is basally dilated, the anthers are basifixed with the connective elliptic and slightly prolongated at the apex, and the pistil has a short style, less than 0.5 mm long. However, *E. harleyi* has long, erect, and crisped hairs on the abaxial surface of the leaves (vs. short, appressed, straight hairs in *E. nitens*), the inner surface of the petals has a continuous band of hairs along the midvein (vs. two tufts of hair at the base and the apex), and a glabrous ovary (vs. hirsute). Furthermore, *E. harleyi* occupies a different habitat (campo rupestre vegetation over white crystalline sand rock, between [500–]800 and 1450 m) and a different geographical area of distribution (Bahia). *Emmotum nitens* is found between 300 and 1000 m in cerrado vegetation on clay soils in the states of Bahia, Distrito Federal, Goiás, Minas Gerais, and Pernambuco in Brazil and the departments of Beni, La Paz, and Santa Cruz in Bolivia. *Emmotum orbiculatum* (Bentham) Miers occurs in the Amazon Basin and is distinguished by its orbicular leaves.

Additional specimens examined. BRAZIL. **Bahia:** área antropizada, *M. L. Guedes et al. 4750* (K, SPF); 4 km S of Mucugê, on rd. from Cascavel by Rio Cumbuca, *R. M. Harley et al. 16055* (K, NY); 4 km S of Mucugê, on rd. from Cascavel by Rio Cumbuca, *R. M. Harley et al. 16056* (K); betw. 2.5 & 5 km S of Vila do Rio de Contas on side rd. to W of the rd. to Livramento, *R. M. Harley et al. 20136* (NY, US); 2–9 km da cidade na estrada a Arapiranga (furna) para o aeroporto, *R. M. Harley et al. 26113* (MO, NY); Serra da Chapadinha, entre Chapadinha e Brejões, *E. Melo et al. 1636* (SPF); arredores de Lençois, caminho para Barro Branco, *S. A. Mori 12940* (A, NY); a 6 km ao SW de Mucugê, *S. A. Mori 13410* (A, NY); Serra das Almas, a 5 km ao NW de Rio de Contas, *S. A. Mori & F. Benton 13526* (A, NY).

3. Emmotum nitens (Benth.) Miers, Ann. Mag. Nat. Hist., ser. 2, 10: 180. 1852. Basionym: *Pogopetalum nitens* Benth., London J. Bot. 2: 377. 1843. TYPE: Brazil. Goiás: s.d., *C. A. Gardner 3309* (lectotype, designated by Duno et al. [2007: 308], K!; isotypes, G!, K!, NY!).

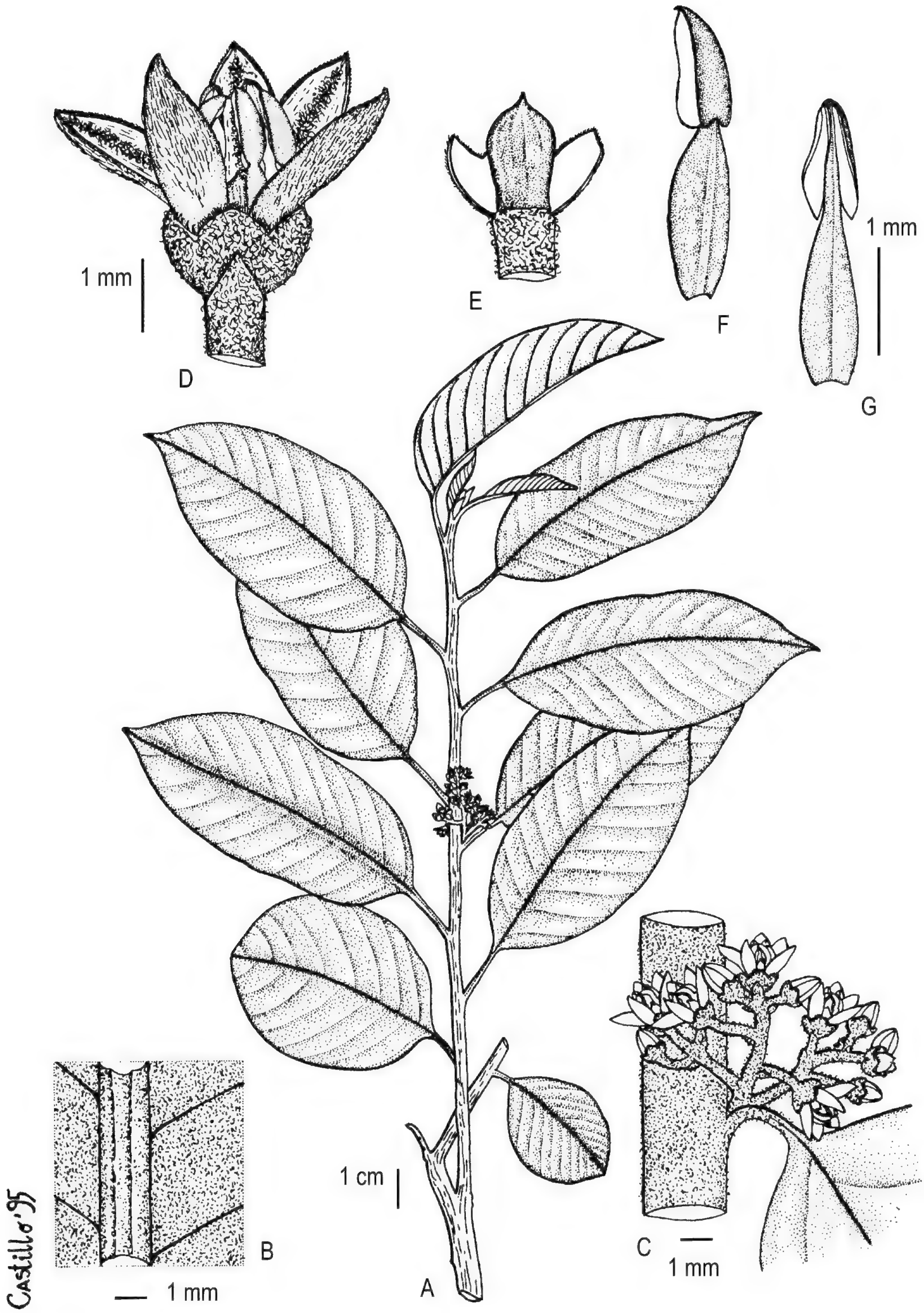

Figure 6. *Emmotum harleyi* Duno. —A. Habit. —B. Detail of the leaf indument (abaxial surface). —C. Detail of the inflorescence. —D. Flower. —E. Detail of the pistil. —F. Stamen, outside surface. —G. Stamen, inner surface. Drawn from the holotype, *R. M. Harley et al. 19248* (K).

Emmotum faia Kuhlm., Arch. Jard. Bot. Rio de Janeiro 26: 45, estampa 1 (s.n). 1982, nom. nud.
Schnizleinia nitida Mart. ex Engl., Fl. Bras. (Martius) 12(2): 46. 1872, nom. nud., in syn.
Siagonanthus sericeus Pohl ex Engl., Fl. Bras. (Martius) 12(2): 46. 1872, nom. nud., in syn.

Shrubs to trees, to 10 m. *Leaves* coriaceous, sharply bicolored, light green or grayish on the abaxial surface, dark green and shiny on the adaxial surface; lamina (5–)6–12 × 3–7 cm, oblong, elliptic, or ovate, apex acuminate to acute, rarely mucronate, base rounded, sericeous, rarely tomentose on the abaxial surface, glabrous on the adaxial surface; secondary veins 6 to 8 pairs, conspicuous; petiole 1.5–2.5 cm. *Inflorescences* with 1- to 5-floriferous branches, up to 4 cm; peduncles to 1 cm. *Flowers* pentamerous; pedicels to 3 mm; *calyx* campanulate, sepal lobes ca. 1.5 × 1.5 cm, triangular to widely triangular; *corolla* with the petals white, 3.5–4 × 1–1.2 mm, narrowly oblong, pilosulose on the adaxial surface, on the base, and near the apex, rarely continuous or glabrous; *stamens* 2.5–3 mm, filaments to 2 mm long, basally dilated; anthers basifixed, connective elliptic, slightly prolongated at the apex; *pistils* 1.5–2 mm, ovary hirsute or glabrous; style up to 0.5 mm, eccentric. *Fruits* ca. 1.5 × 1.5 cm (diam.).

Distribution and ecology. *Emmotum nitens* is found in Brazil (Amazonas, Bahia, Distrito Federal, Goiás, Maranhão, Mato Grosso, Minas Gerais, Pará, and Pernambuco) and Bolivia (Beni, La Paz, and Santa Cruz). It grows in savannas (cerrado) between 300 and 1000 m elevation.

Phenology. Flowering and fruiting occur year round.

IUCN Red List category. *Emmotum nitens* is a common species in the Brazilian cerrado. It occurs along a continuous area of ca. 2,000,000 km^2. There are numerous botanical collections, including some made inside protected areas. Despite the fact that the cerrado is one of the most threatened ecosystems in Brazil, the populations of this species seem to be large enough for this species to be excluded from any category of protection according to IUCN Red List criteria (IUCN, 2001), or alternatively could be listed as Least Concern (LC).

Vernacular names and uses. In Brazil it is known as faia (Ferreira & de Abreu, 1982; Corrêa, 1984).

Discussion. In the current phylogenetic analysis, *Emmotum nitens* is the sister species of *E. orbiculatum*. These two species, together with *E. amazonicum* and *E. harleyi*, form a very distinct clade based on the combination of petals pilose on the abaxial surface with two clusters of hair at the base and the apex or almost glabrous, stamens with the filament dilated at the base, the anthers basifixed with the connective elliptic and slightly prolongated at the apex, and the ovary with a short style, less than 0.5 mm long. *Emmotum orbiculatum* has widely oblongate, widely elliptic, or widely ovate lamina with the apex mucronate. *Emmotum amazonicum* has an elliptic to elliptic-oblong lamina and a glabrous ovary.

The authors of *Emmotum faia* (Ferreira & de Abreu, 1982) did not explicitly typify the name, thus making it invalid under Article 37.1 of the *International Code of Botanical Nomenclature* (McNeill et al., 2006). However, it is obvious from the description and illustration that this entity is referable to *E. nitens*.

Additional specimens examined. BRAZIL. **Amazonas:** Rio Tarumá, cachoeira baixa, *A. Ducke 1413* (IAN, MG, NY, US). **Bahia:** Serra ca. 30 km W of Barreiras, *W. R. Anderson et al. 36528* (F, MO, US); Espigao Mestre, ca. 100 km WSW of Barreiras, *W. R. Anderson et al. 36782* (F, MO, NY); Serra Acurua, *Blanchet 2889* (BM, G, GH, NY, US); entre Ajuda e Porto Seguro, *A. P. Duarte 6636* (CTES); entre Brejao e Iracema, regiao de Serra Sincorá, *R. L. Fróes 20196* (NY, US); 2–9 km da cidade na estrada a Arapiranga (furna) para o aeroporto, area de inundaçao da Barragem do Sao Bartolomeu, Rio Taboca, *E. P. Heringer et al. 1383* (MO, R, US); Bacia do Rio Sao Bartolomeu, *E. P. Heringer et al. 1791* (K, MO, NY, US); Córrego, capoeira do Bálsamo, 10 km E of Brasilia, *H. S. Irwin et al. 8378* (F, GH, MO, NY); vic. Paranóa, *H. S. Irwin et al. 11253* (F, GH, MO, NY, US); 10 km NW of Planaltina, *H. S. Irwin et al. 13190* (F, GH, MO, NY); Córrego Alogado, Parque Mun. Gama, ca. 20 km SW of Brasilia, *H. S. Irwin et al. 14098* (F, G, GH, MO, NY, US); rodovia a Livramento do Brumado/Rio de Contas, *S. A. Mori et al. 12280* (A, US); Nova Rodovia Andarai/Mucugê, a 15–20 km ao S de Andarai, *S. A. Mori & F. P. Benton 13119* (A, NY). **Espírito Santo:** Reserva Florestal da CVRD, Linhares Esp. Santo Est. Flamengo, ant. x-1, Km 4232, lado esquerdo, *G. L. Farias 50* (A); Reserva Florestal da CVRD, Linhares, P. Sapo, ant. 161, Km 0.06, lado esquerdo, *D. A. Folli 73/79* (A). **Goiás:** Serra dos Cristais, 5 km by rd. of Cristalina, *W. R. Anderson et al. 8162* (A, NY); Serra Dourada, ca. 15 km (straight line) S of Goiás Velho, *W. R. Anderson et al. 10048* (A, AAU, MO, NY, US); 26–31 km S of Goiania along Hwy. BR-153, *G. T. Davidse et al. 12260* (AAU, NY, PMA, US); Contraforte Central, ca. 24 km NE of Catalao, *H. S. Irwin et al. 25385* (F, MO, NY, US); Serra Geral do Paraná, 20 km S of Sao Joao de Alianza, *H. S. Irwin et al. 32102* (A, MO, NY); Caiaponia, 9 km S, *P. I. Oliveira 401* (GB); W of Filadelfia on Serra de Mamoneira, *G. T. Prance & N. T. Silva 58521* (A, F, NY, US); 35 km S of Caiaponia, Serra do Caiapó, *G. T. Prance & N. T. Silva 5968* (A, F, NY, US); entre Jataí Caiaponia, ca. 123 km de Jataí, em frente a serra de Caiapó, 2 Oct. 1968, *Sidney & Onishi 1023* (A [2]); Meia Ponte, *E. Ule s.n.* (R). **Maranhão:** Ilha de Balsas, region betw. Balsas & Parnaíba rivers, 13 km SSE of Loreto, *G. Eiten & L. T. Eiten 10803* (K, NY, US); a 2 leugas de Carolina, *J. M. Pires & G. A. Black 1607a* (US). **Mato Grosso:** estr. Santarém–Cuiabá,

BR 163, Km 762, 30 km de Guarantan, Serra de Cachimbo, *I. L. Amaral et al. 823* (A, MO, NY); 25 km S of Xavantina, *H. S. Irwin et al. 17086* (F, GH, MO, NY, US); 70 km S of Xavantina, *H. S. Irwin et al. 17452* (F, GH, MO, NY, US); 0.5 km SE of base camp, *D. Philcox et al. 3351* (K, MO, NY); Sararé, *J. M. Pires & M. R. Santos 16402* (F, GH, MO, NY). **Minas Gerais:** Serra do Espinhaço at Lapinha, ca. 19 km N of Sêrro on rd. to Diamantina, *H. S. Irwin et al. 20808* (F, G, NY); 33 km SW of Diamantina, near Gouveia, *H. S. Irwin et al. 22289* (F, K, NY); alrededor de Itapanhoacanga, base de la Serra do Espinhaco, *M. M. Mello-Silva et al. 4322* (CTES); 30 km de Felixlandia para Brasilia, *J. M. Pires 57974* (A, MO, NY); Caratinga, Estação Biol. caratinga, *K. B. Stier 697* (A, NY). **Pernambuco:** Rio Petro, 1 Jan. 1838, *C. A. Gardner 2941* (K). BOLIVIA. **Santa Cruz:** Parque Nacional Noel Kempff Mercado, ca. camp. viejo de los Fierros, 3–5 km N del camino principal entre Los Fierros y Tarbo, sobre el camnio a la meseta, *M. S. Arroyo 2829* (CTES); camp. Toledo, a 100 m al E de la casa, yendo hacia el río Paragúa, *R. Guillén & V. Choré 1872* (NY, USZ); Parque Nacional Noel Kempff Mercado, Los Fierros, 5–8 km al NE de la carretera, *T. Killen et al. 5642* (NY, USZ); Reserva Ecologica El Refugio, a 10 km hacia Los Fierros, *T. Killen et al. 6725* (MO); Estación Flor de Oro, W side of Río Guaporé [Río Iténes], 0–1 km W of airstrip, *M. Nee 41218* (GH, LBP, NY); 3 km NW of buildings at Estación Oro, along oxbow lake along Río Iténez [Río Guapor], *M. Nee 41458* (GH, NY); Estación Flor de Oro, margen del Río Iténez (Guaporé), frontera con Rondonia, 20 km N de Serranía de Huanchaca, 85 km E del Río Paragua, *M. Peña & R. Foster 172* (F, MO, NY); Serranía de Huanchaca, Parque Nacional Noel Kempff Mercado, 5–7 km al S del Río Itenes o Guaporé, 15 km SE del Estación de Flor, *M. Toledo 50* (F, USZ).

4. **Emmotum orbiculatum** (Benth.) Miers, Ann. Mag. Nat. Hist., ser. 2, 10: 178. 1852. Basionym: *Pogopetalum orbiculatum* Benth., Proc. Linn. Soc. London 1(10): 88. 1841. TYPE: Guyana. Dry savannahs on Padawire River, s.d., *R. Schomburgk s.n.* (holotype, K!).

Emmotum holosericeum Ducke, Arch. Inst. Biol. Veg. 4: 45. 1938. TYPE: Brazil. Amazonas: Borba, Rio Madeira, *A. Ducke 35548* (holotype, BR!; isotypes, K!, U not seen, US!).

Shrub or trees, 3–12 m. *Leaves* coriaceous, sharply bicolored, light green or yellow on the abaxial surfaces and dark green and shiny on the adaxial surface; lamina 10–22 × 6–13 cm, widely oblongate, widely elliptic, or widely ovate, sericeous or velvet on the abaxial surface, apex mucronate to shortly acuminate, sometimes retuse, base rounded; secondary veins 8 to 9 pairs, conspicuous; petiole 1–2 cm. *Inflorescences* axillary, 1- to 4-floriferous branches, up to 3 cm, sericeous; peduncle up to 1 cm. *Flowers* pentamerous; pedicels up to 3 mm; *calyx* campanulate, sepal lobes ca. 1.5 × 1.5 cm, widely triangular; *corolla* with the petals 4–4.5 × 1–1.2 mm, narrowly oblongate, bearded on the adaxial surface, on the base, and near the apex, rarely continuous or glabrous; *stamens* 4–4.5 mm, filaments to 2 mm long, swelled; anther 1–1.2 mm, basifixed, connective elliptic, apex slightly prolongated; *pistils* 2–2.5 mm, ovary hirsute, base glabrous; style up to 0.5 mm, centric. *Fruits* ca. 1.5 × 1.5 cm (diam.).

Distribution and ecology. *Emmotum orbiculatum* ocurrs in Colombia (Vaupés), Guyana, and Brazil (Amazonas and Roraima). It grows in forests at 100 m elevation.

Phenology. *Emmotum orbiculatum* flowers year around and fruits from (March to) May to December.

IUCN Red List category. *Emmotum orbiculatum* is a common species in the Brazilian Amazon Basin. There are numerous botanical collections, including some from inside protected areas. Therefore, this species could be excluded from any category of protection according to IUCN Red List criteria (IUCN, 2001), or alternatively could be listed as Least Concern (LC).

Discussion. *Emmotum orbiculatum* is similar to *E. amazonicum* and *E. nitens* in having the base and apex of the filament dilated, the anthers oblong-linear with the connective elliptic and prolongated, and the ovary with a short style, less than 0.5 mm long. *Emmotum holosericeum*, a species here referred to the synonymy of *E. orbiculatum*, is only known from the type specimens. Ducke (1938) considered the indument characters of this sterile specimen different enough to propose a new species. Here we follow the de Roon (1994) point of view in referring *E. holosericeum* to the synonymy of *E. orbiculatum*, because a similar pubescence pattern has been observed in some other species of this clade, such as *E. nitens*.

Additional specimens examined. BRAZIL. **Amazonas:** Rio Cuieiras, Rio Cuieiras near mouth of rio Branchinho, *A. B. Anderson 92b* (MO, NY), *A. B. Anderson 178* (MO, NY); Manaus–Caracarai Rd., Km 140, *C. C. Berg et al. P18177* (A, NY). **Roraima:** entre Km 350 e 355 da Estr. Manaus–Caracaraí (BR 174), *C. A. Cid Ferreira 9068* (F, GH, NY); rodovia perimetral N 20 km E de Caracaraí, *J. M. Pires & P. Leites 14843* (A, INPA); BR 174, Manaus–Venezuelan Hwy., Estr. Manaus–Caracarai, Km 350, N of Rio Branchinho, *W. C. Steward et al. 80* (A, F, NY, US). COLOMBIA. **Vaupés:** Rio Kuduyari, *H. García Barriga et al. 15837* (K). GUYANA. Rio Padawire, *Schomburg 231* (K).

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APPENDIX 1. Characters and character states used in the cladistic analysis of *Emmotum*.

1. Habit: tree (0), shrub (1).
2. Pigment in chemical reaction of the flower in alcohol: absent (0), red (1), black (2).
3. Malpighiaceous hairs: present (0), present but arms unequal (1), absent (2).
4. Articulated hairs: absent (0), present (1).
5. Length of the petiole (cm): 0.4–0.8 (0), 1–2.5 (1).
6. Length of the lamina (cm): 2–5 (0), 6–20 (1).
7. Form of the apex of the leaves: acute (0), narrowly acute (1), rounded (2).
8. Bicolorous leaves: no (0), yes (1).
9. Number of pairs of secondary veins: (0) 2 to 3, (1) 5 to 15.
10. Patent secondary veins: no (0), yes (1).
11. Persistent pubescence of the leaves: no (0), yes (1).
12. Number of flower parts: tetramerous (0), pentamerous (1).
13. Inflorescence: spike (0), cyme (1), panicle (2).
14. Sexuality: unisexual (0), bisexual (1).

15. Number of flowers: 1 to 3 (0), 10 to 20 (1), 50 or more (2).
16. Sepal aestivation: imbricate (0), valvate (1).
17. Flower color: greenish to yellowish (0), white (1).
18. Internal grooves of the petals present: no (0), yes (1).
19. Petal connation: joined at the base (0), free (1).
20. Petal texture: thickened (0), slightly developed (1), membranous (2).
21. Petals with cylindrical hairs on the inner surface: no (0), yes (1).
22. Cylindrical hairs continuous on the inner surface: yes (0), no (1).
23. Shape of the filament: obovate (0), narrowly ovate (1), ovate (2), filiform (3).
24. Length of the filament (mm): absent (0), 1.5–2 (1), 3.5–5 (2).
25. Anthers (attachment): basifixed (0), dorsifixed (1).
26. Anthers (shape): oblong (0), sagittate (1), cordate (2), globose (3).
27. Apex of the filament: attenuated (0), dilated (1), as wide as the middle section (2).
28. Ratio length of the anther and filament: anther is several times longer than the filament, more than 5:1 (0), anther is as long as the filament, 1:1 (1), anther is about half as long as the filament, 1:2 (2), anther is three or four times smaller than the filament, 1:3–4 (3).
29. Connective (shape): very broadly ovate (0), broadly ovate (1), elliptic (2), ovate (3), absent (4).
30. Connective (prolongation): long (0), short (1), absent (2).
31. Ring of tissue around the base of the ovary: no (0), yes (1).
32. Length of the style (mm): absent (0), 0.1–0.5 (1), 2.5–4 (2), 5 or more (3).
33. Style position: central (0), lateral (1).
34. Ovary (type): unilocular (0), multilocular (1).
35. Ovary (pubescence): no (0), yes (1).
36. Fruit (shape): oblong (0), globose (1).
37. Fruit (size, cm): more than 3 (0), less than 1.5 (1).
38. Mesocarp (fleshy): present, very well developed (0), present, tiny (1), absent (2).
39. Fruits (apex): rounded or acute (0), shortly mucronate (1), acute (2).
40. Endocarp (suture): absent (0), present, slightly developed (1), present, very well developed (2).
41. Embryo (size): small (0), big (1).

Comments about the characters and character states:

[2] Pigment in chemical reaction of the flower in alcohol: When flowers and leaves are soaked in 50% alcohol, the liquid turns red or black, or else remains unchanged. Despite the fact that the biochemical nature of these processes is unknown to us (most likely an oxidative phenolic reaction), we considered this coloration as an alternative state of a single chemical character. In *Oecopetalum* and *Ottoschulzia* the pigment remains unchanged (0); in all species of *Poraqueiba* and *Emmotum* it turns red (1); and in *Calatola* the liquid becomes black (2).

[8] Bicolorous leaves: When specimens of Icacinaceae dry, some have bicolorous leaves; this occurs in some taxa of *Emmotum* sect. *Emmotum*, all members of *Emmotum* sect. *Brevistyla*, and some members of the outgroup. It does not occur in *Calatola* (dries completely black), *Oecopetalum* and *Poraqueiba* (dries yellow-brown), and *Ottoschulzia* (dries brown).

[13] Inflorescence: The main inflorescence of the Icacinaceae taxa is a panicle, but in *Calatola* the male inflorescence has flowers without pedicels giving rise to a spike (0); in *Ottoschulzia* and *Oecopetalum* the inflorescence has a terminal flower giving rise to a cyme (1), with few flowers in the first genus and many flowers in *Oecopetalum* (see character 15 below). In *Poraqueiba* and *Emmotum* the inflorescence is the generalized panicle of the family (2).

[14] Sexuality of flowers: The Neotropical genera of Icacinaceae are mainly monoecious plants with bisexual flowers (1), but *Calatola* has dioecious and unisexual flowers (0).

[15] Number of flowers: The number of flowers per inflorescence is variable among genera. In *Ottoschulzia* the inflorescence is reduced to one to three flowers (0); in *Emmotum* and *Poraqueiba* the number of flowers per inflorescence varies from 10 to 20 (1), but in *Calatola* and *Oecopetalum* it increases to more than 50.

[18] Internal grooves of the petals present: The petal of some of these taxa has the abaxial surface with special kinds of structures. We reduce this morphological complex character to a binary situation. In *Ottoschulzia*, *Oecopetalum*, and *Poraqueiba* there is a very well-developed internal groove (1), while in *Calatola* and *Emmotum* the internal surface of the petals lacks any kind of appendages (0).

[21] Cylindrical hairs on the inner surface of the petals: The typical indument in the inner petal face of *Emmotum* is due to the presence of cylindrical hairs (1), but in all taxa of the outgroup this indument is absent or made up of other kinds of ornamentation (0).

[22] Cylindrical hairs continuous: This character does not apply to all members of the family, only to members of the genus *Emmotum* (see character 21, above). In *Emmotum* two types of indument can be observed on the inner face of the petal. In members of *Emmotum* sect. *Emmotum* the indument is dense and continuous from the base to the apex (0), while in members of *Emmotum* sect. *Brevistyla* the indument is reduced to two tufts of hairs on the base and the apex (1). For the outgroup, the character was recorded as not applicable (?).

[23] Shape of the filament: The outline of the filament is variable between genera of the Icacinaceae family. In *Poraqueiba* it is massive, fleshy, thick, and obovate (0); in *Oecopetalum* and *Ottoschulzia* it is slightly fleshy, thick, and narrowly ovate (1); in *Emmotum* it is slightly thickened and ovate (2), and in *Calatola* it is filiform (3).

[24] Length of the filament (mm): This continuous character can be scored in three discrete states; in *Calatola* the filament is almost absent (0); in members of *Emmotum* sect. *Brevistyla* it is medium sized and 1.5–2 mm long (1); and in members of *Emmotum* sect. *Emmotum*, *Oecopetalum*, and *Ottoschulzia* it is 3.5–5 mm long (2).

[26] Anthers (shape): The outline of the anther is variable in *Emmotum* and other members of the outgroup. In *Poraqueiba* the anther is oblong (0), sagittate in *Oecopetalum* and *Ottoschulzia* (1), cordate in *Emmotum* (2), and globose in *Calatola* (3).

[27] Apex of the filament: The apex of the filament is variable within *Emmotum* and members of the outgroup. This character is better understood if we describe the apex as compared with the middle portion of the filament. Thus, in *Poraqueiba* and in members of *Emmotum* sect. *Brevistyla* the apex is attenuated, narrower than the middle section (0), in *Emmotum* sect. *Brevistyla* the apex is dilated, much broader than the middle section (1), and in *Calatola* it is as wide as the middle section (2).

[28] Ratio of anther length:filament length: There is a significant difference between the size of the filament and anther, and these differences can be expressed in relation to its proportion. In *Calatola* the anther is several times longer than the filament, more than 5:1 (0). In members of *Emmotum* sect. *Brevistyla*, the anther is as long as the filament and the ratio is 1:1 (1). In *Poraqueiba* the anther is about half as long as the filament, with a ratio of 1:2 (2). In members of *Emmotum* sect. *Emmotum*, *Oecopetalum*, and *Ottoschulzia*, the anther is three or four times smaller than the filament, 1:3–4 (3).

[29] Connective shape: There are important differences in the shape of the connective. In *Poraqueiba* it is very broadly ovate (0), in *Oecopetalum* and *Ottoschulzia* it can be defined as broadly ovate (1), in members of *Emmotum* sect. *Brevistyla* it is elliptic (2), in members of *Emmotum* sect. *Emmotum* it is ovate (3), and in *Calatola* it is absent (4).

[30] Connective (prolongation): In general the apex of the connective does not extend to the anther, but it is massive and long in *Poraqueiba* (0), short in members of *Emmotum* sect. *Brevistyla* (1), and absent in members of *Emmotum* sect. *Emmotum*, *Oecopetalum*, *Ottoschulzia*, and *Calatola* (2).

[31] Ring of tissue around the base of the ovary: In general in all members of *Emmotum* and the outgroup there is no difference in the base around the ovary (0), but in two species, *E. acuminatum* and *E. floribundum*, there is a diminute ring of tissue surrounding the base of the ovary (1).

[32] Length of the style (mm): The length of the style is variable in members of *Emmotum* and the outgroup, and it is particularly important in members of *Emmotum*. In *Calatola*, the style is absent (0); in members of *Poraqueiba* and *Emmotum* sect. *Brevistyla* the style is short, less than 0.5 mm long or smaller than the ovary (1); in members of *Emmotum* sect. *Emmotum* the style is long, 2.5–4 mm or twice as long as the ovary (2); in *Oecopetalum* and *Ottoschulzia* the style is longer, ca. 5 mm (3).

[33] Style position: In general, in all members of *Emmotum* and the outgroup the style is central (0), but in two species of *Emmotum*, *E. acuminatum* and *E. floribundum*, the style is displaced somewhat sideways, becoming eccentric or lateral (1).

STUDIES IN THE CLEOMACEAE I. ON THE SEPARATE RECOGNITION OF CAPPARACEAE, CLEOMACEAE, AND BRASSICACEAE[1]

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Abstract

Molecular data support the recognition of three monophyletic families, Capparaceae s. str., Cleomaceae, and Brassicaceae, instead of an all-encompassing Brassicaceae or a paraphyletic Capparaceae s.l. This view is reinforced with many figures showing two basic and ubiquitous differences in cleomoid seed structure. First, the more or less strongly incurved seed, varying from reniform to horseshoe-shaped, coiled or conduplicate, uniformly and in all species, results in a deep invagination of the testa (the cleft) projecting into the interval between the two ends, or claws, of the embryo (this invagination is absent or rarely reduced and atavistic in Brassicaceae, and infrequent in Capparaceae s. str., i.e., in some *Capparis* L. species and *Crateva* L., sister genus to all remaining Capparaceae s. str.). Second, the uniformly semicylindric, strictly incumbent cotyledons are small and narrow, but are never foliaceous and interfolded, circinate or convoluted, or massive and thick, as in the often accumbent, rarely incumbent Capparaceae, or as variable as in Brassicaceae. An illustrated glossary of Cleomaceae seed morphology, as well as depictions of Capparaceae, Cleomaceae, and Brassicaceae seeds and their sectional views, and a key to all three families, are included.

Key words: Brassicaceae s. str., Brassicales, Capparaceae s. str., Cleomaceae, embryo morphology, familial realignments, seed structure.

Brassicaceae and Capparaceae s.l. have long been thought to be closely related families, a relationship that is supported by morphological and chemical data (Fig. 1; e.g., Iltis, 1957; Rodman et al., 1993, 1994, 1996; Rollins, 1993; Hall et al., 2002). Until recently, the approximately 45 genera and 800 species of the pantropical family Capparaceae s.l. have been classified into two major subfamilies, Capparoideae and Cleomoideae (Pax & Hoffmann, 1936; Melchior, 1964). However, molecular and morphological phylogenetic analyses of the family and relatives reveal that Capparaceae as traditionally circumscribed are paraphyletic, with the larger, mostly temperate family Brassicaceae embedded within it (Rodman et al., 1993, 1994, 1996; Judd et al., 1994; Hall et al., 2002, 2004). Chloroplast sequence data strongly support the monophyly of the three lineages: Brassicaceae s. str., Capparaceae subfam. Capparoideae, and Capparaceae subfam. Cleomoideae, with strong support for a sister relationship of Cleomoideae to Brassicaceae (Hall et al., 2002, 2004; Hall, 2008).

Thus, phylogenetic relationships inferred from chloroplast sequence information (*ndhF*, *trnL-trnF*, *matK*, and *rbcL*) and the criterion of monophyly permit three alternatives for familial recognition (Fig. 1): (A) three families, Brassicaceae s. str., Cleomaceae, and Capparaceae s. str.; (B) two families, Brassicaceae (including Brassicaceae s. str. and subfamily Cleomoideae) and Capparaceae (represented only by subfamily Capparoideae); and (C) one single family, Brassicaceae s.l. (Angiosperm Phylogeny Group, 1998, 2003; including Brassicaceae s. str. and Capparaceae s.l. and subfamily Cleomoideae; see Judd et al., 1994 for arguments on the priority of the name Brassicaceae over Capparaceae). In more recent literature, two of these alternatives are prevalent. Some authors merge all three into one, all-inclusive Brassicaceae (Angiosperm Phylogeny Group, 1998, 2003; Judd et al., 1994, 2007), whereas

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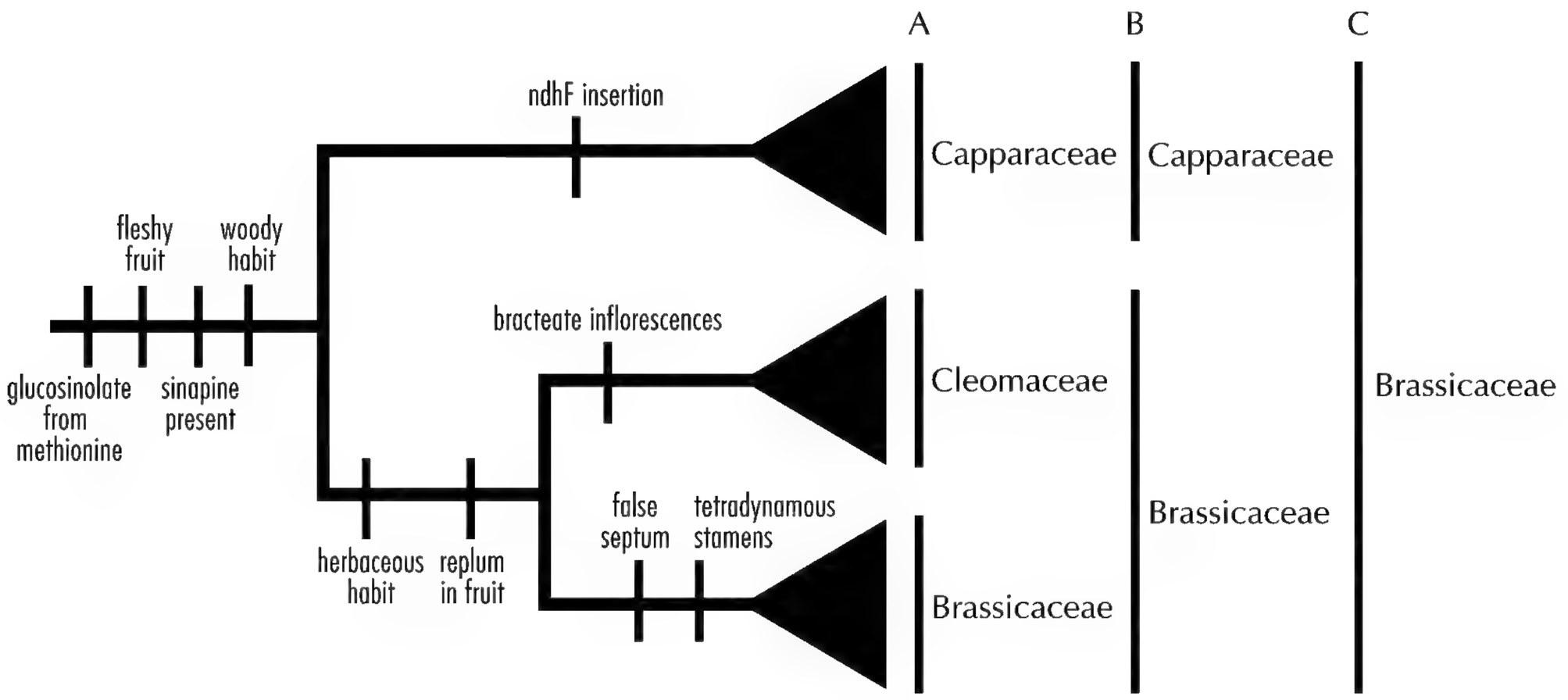

Figure 1. Three scenarios (cf. family names at right) for family recognition in the Brassicaceae, Cleomaceae, and Capparaceae clade consistent with molecular data. Distinguishing morphological characters are placed to represent synapomorphies (shared derived character states). Adapted from Hall et al. (2002: 1840).

others recognize three separate families (Hall et al., 2002; Simpson, 2006; Heywood et al., 2007), the concept now adopted by the Angiosperm Phylogeny Group (2009). Here, we argue that it would be much less disruptive and practical to recognize three monophyletic families.

In addition to the criterion of monophyly, there are other considerations to take into account when establishing familial boundaries. These factors include stability, ease of identification, and level of support for monophyly (Backlund & Bremer, 1998). The Brassicaceae s. str. are a cohesive and easily identifiable family. In fact, in light of the distinctive morphological features of its members, Brassicaceae have been one of the few families to be recognized as such throughout recorded history (Rollins, 1993). The Cleomaceae are also readily identifiable (see key below). Recent phylogenetic studies are making Capparaceae s. str. more cohesive, with many of the morphologically inconsistent taxa having been removed (e.g., *Setchellanthus* Brandegee to its own family Setchellanthaceae: Carlquist & Miller, 1999; Iltis, 1999; Karol et al., 1999; Tobe et al., 1999; Tomb, 1999; *Physena* Noronha ex Thouars to its own family Physenaceae: Takhtajan, 1985; *Stixis* Lour. [including *Roydsia* Roxb.], *Tirania* Pierre, *Neothorelia* Gagnep., and *Forchhammeria* Liebm. to one or more small families, the classification yet to be worked out: Kers, 2003; Hall et al., 2004). In addition, the elevation of the two subfamilies of Capparaceae to familial status had been suggested and accepted some 40 years ago by previous taxonomists (Airy Shaw, 1965; Hutchinson, 1967).

Although there are many clear morphological synapomorphies for Brassicaceae and Cleomaceae (Figs. 1, 2I–Z, 3; key to the three families), those for Capparaceae are more elusive (Figs. 1, 2A–H). Despite the lack of clear morphological synapomorphies, Capparaceae can easily be distinguished from Brassicaceae and Cleomaceae (key below; Table 1) by

Table 1. Morphological comparison of Capparaceae, Cleomaceae, and Brassicaceae.

	Capparaceae s. str.	Cleomaceae	Brassicaceae s. str.
Habit	woody	herbaceous, rarely woody	herbaceous, rarely woody
Leaf structure	simple, occasionally compound	compound, rarely simple	simple, rarely compound
Fruit morphology	fleshy capsules or berries, indehiscent (usually) or dehiscent, rarely with a replum	dry capsules, dehiscent with a replum, very rarely indehiscent	dry siliques or silicles, dehiscent with a replum and false septum, rarely indehiscent, sometimes transverse-jointed
Arils	often present	sometimes present	rarely present
Seed shape	globose to ovoid, ellipsoid, or reniform, testa shallowly or not invaginated	mostly reniform to reniform-orbicular or horseshoe-shaped, testa deeply invaginated	various, commonly globose, ovoid, or oblong, often (somewhat) flattened, lacking a cleft or testa not deeply invaginated
Cotyledons	incumbent to accumbent	incumbent	incumbent, accumbent, conduplicate or spirally coiled

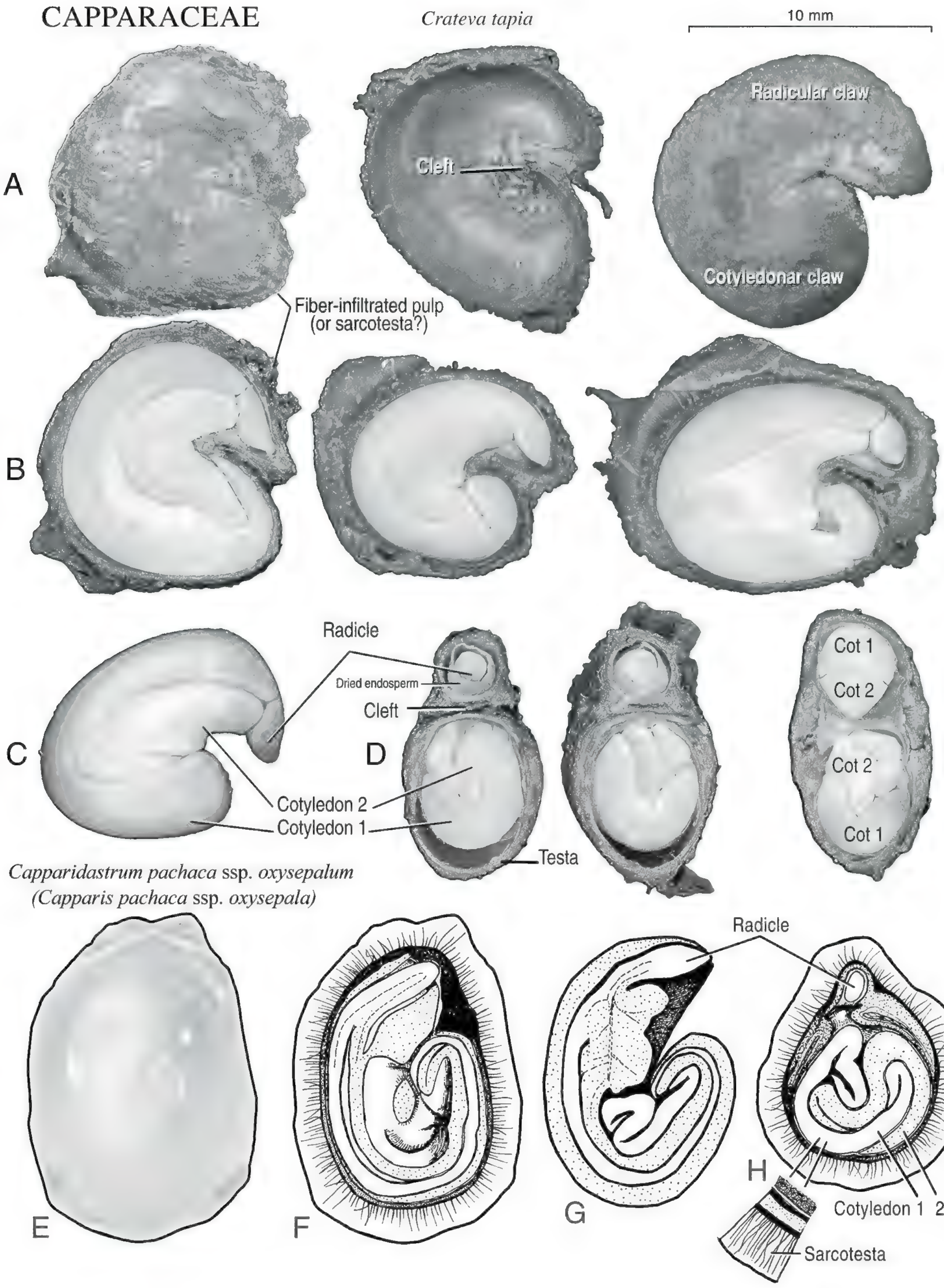

Figure 2. Seed morphology in Brassicales: configurations of embryo and testa. A–H. Seeds of New World Capparaceae. A–D. *Crateva tapia* L. (Nicaragua, Chontales, *Nee 28459* [WIS]). —A. Seeds, exterior views, surrounded by irregularly shaped, pulpy, densely hair-infiltrated sarcotestas. —B. Longitudinal sections of seeds (A, at left, and B, at left, views of the same seed), showing the very short, conical radicle sharply differentiated from the cotyledons by deep constrictions; the strongly asymmetrical connections of the two cotyledons to the radicle; and the greater length and thickness of the outer cotyledon, which obliquely embraces the inner and, at its tip, curves around and over the latter. —C. Whole embryo (views of the same seed as A and B at left and above), with testa removed. —D. Cross sections of seeds. D views at left and center represent the two halves of the same seed sectioned through the radicle and the near far ends of the convoluted cotyledons, to show the J-shaped cotyledon 1 obliquely embracing cotyledon 2. D view of seed at far right is sectioned through the base of the cotyledons just above the radicle, where only here they are shown to be, at least at the base, strictly incumbent. (Caption continued on next page.)

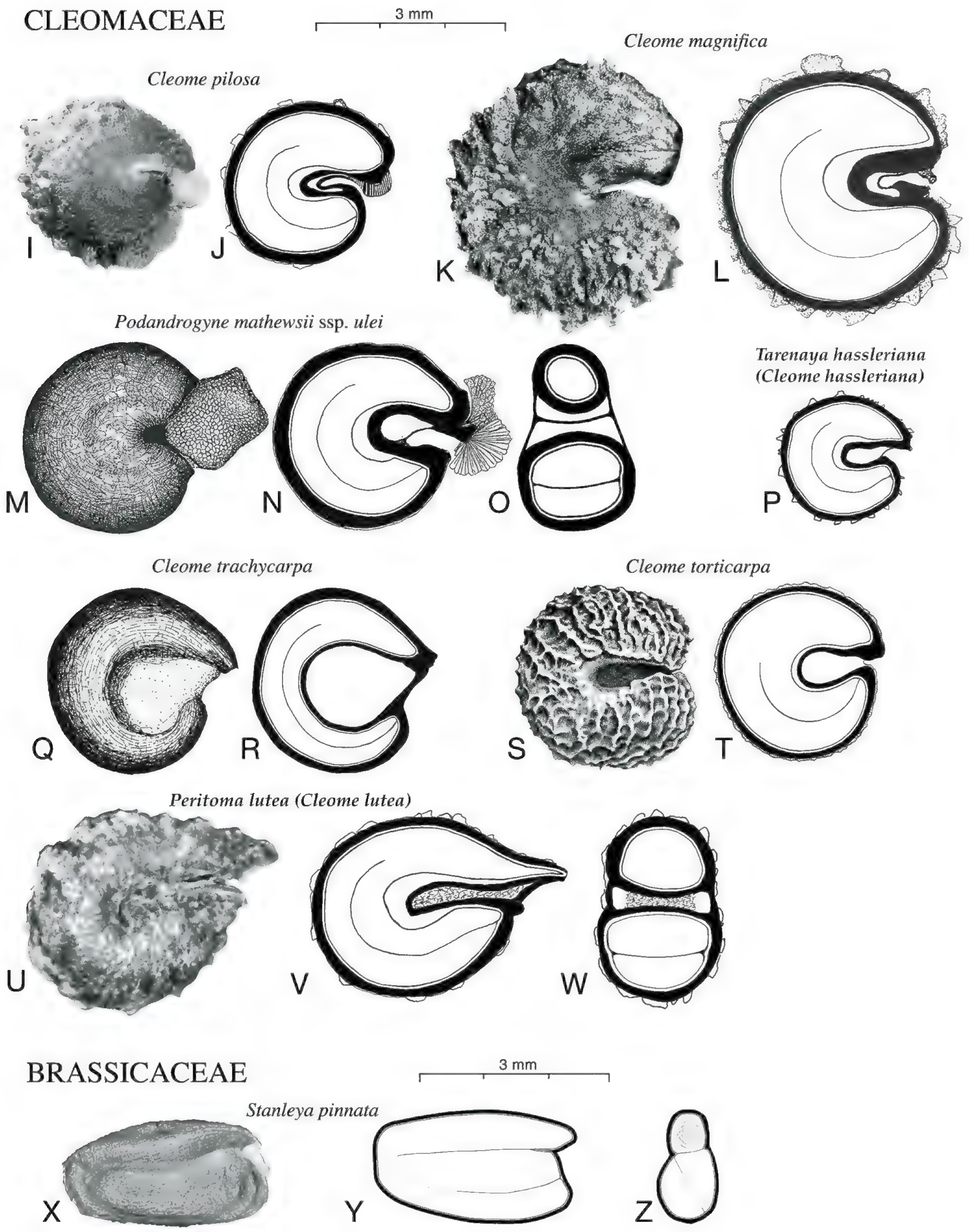

Figure 2. Continued. E–H. *Capparidastrum pachaca* (Kunth) Hutch. subsp. *oxysepalum* (C. Wright ex Radlk.) Iltis (Mexico, Oaxaca, *King 1479* [WIS], from Iltis, 1965: 60, cf. for detailed description; cf. also Cornejo & Iltis, 2008b). —E. Seed, exterior view, surrounded by a jellified, opaque, hair-infiltrated sarcotesta. —F. Longitudinal diagram of E. —G. Diagram of conduplicate embryo only. —H. Cross section of E, showing views as in F–H, with the two basally incumbent but distally convoluted cotyledons wrapped around each other and the radicle (hence the embryo conduplicate) and, as in F, the absence of a significant testa invagination between radicle and cotyledons. This is the usual condition in many species of Capparaceae (e.g., *Cynophalla flexuosa* (L.) J. Presl [= *Capparis flexuosa* (L.) L.]). I–W. Seeds of New World Cleomaceae. —I–L. *Cleome pilosa* Benth. (I, J) and *C. magnifica* Briq. (K, L). Both show the deep invagination of the testa forming the seed cleft and, into it, the secondary invagination of the cleft membrane, resulting in a small, internal cleft chamber and a short, open outer cleft. *Cleome pilosa* bears a small, funicular aril at the tip of the radicular claw, the probable precursor of that peculiar structure in *Podandrogyne* Ducke. —M–O. Seed of *P. mathewsii* (Briq.) Cochrane subsp. *ulei* (Briq.) Cochrane, a member of a speciose genus closely related to *Cleome*, characterized, inter alia, by arillate seeds semipersistent on the replum and presumably dispersed by ants (Iltis & Cochrane, 1989; Cochrane, 1997, 2011). P–T. (Caption continued on next page.)

the retention of a number of plesiomorphic characters, including woody habit, fleshy fruits with often arillate or sarcotestate seeds, and, rarely, compound trifoliolate leaves (e.g., *Crateva* L., some species of *Ritchiea* R. Br. ex G. Don, *Thylachium* Lour., and *Maerua* Forssk.). Although palmately compound leaves in *Crateva* have been suggested as a synapomorphy for Cleomaceae (Judd et al., 1994), the presence of this character state in *Crateva*, a genus that is sister to all other Capparaceae (Hall et al., 2002; Hall, 2008), contradicts this synapomorphy. In addition, compound leaves occur in the other closely related families in the order, Tovariaceae and Forchhammeriaceae nom. ined. (e.g., *Forchhammeria trifoliata* Radlk.).

The Cleomaceae differ from both Capparaceae and Brassicaceae by uniformly strongly curved, reniform or horseshoe-shaped to conduplicate seeds with an incurved embryo with always strictly incumbent cotyledons, in which its two ends are always separated by a deep invagination of the testa, the cleft (Fig. 2I–W; Sánchez-Acebo, 2005: 188–192, figs. 4–7; Iltis, Cochrane & Tucker, unpub.: figs. 1, 3). In most Capparaceae that have been studied (New World representatives), however, this testa invagination is usually shallow and obsolete, or simply consists of a very short, scalelike projection from inside the testa that does not intrude deeply into the embryo. Moreover, the embryos (but not the seeds) of Capparaceae are often sharply conduplicate, as if derived from reniform or conduplicate seeds in which the testa invagination has been deleted. Thus, these typically conduplicate embryos of Capparaceae sometimes appear straight (in species with elongate siliques) or spherical (in round berry fruits), but with the convoluted, often circinate and foliaceous cotyledons variously folded or wrapped around both each other and often around the radicle as well, in a complicated fashion (Fig. 2A–H; Eichler, 1865: tab. 64, 65; Iltis et al., 1996: 380, fig. 1D), thus often betraying their evolutionary origins in cleomoid-like seeds.

Crateva are of particular interest because the phylogenetic position of the genus as sister to all remaining Capparaceae may provide insight on putative primitive character states. Specifically, there are significant cleomoid characteristics of the *Crateva* seed that support the strongly curved, deeply invaginated reniform seed as a plesiomorphic character. Among the exceptions are the capparoid embryos inside of the cleomoid seeds of *Crateva* (e.g., *C. tapia* L.) that, strongly curved, from reniform to conduplicate, have a profound, wide to narrow invagination of the testa projecting deeply into the embryo, sometimes as deep as the seed's center or even beyond (Fig. 2A–D). Curiously, with the *Crateva* radicle-hypocotyl axis being conical and exceedingly short (in *C. tapia* only 1.5–2 mm; cf. Fig. 2B), and with its basally incumbent yet irregularly ill-fitted and somewhat unequal cotyledons filling more than nine tenths of the curvature of the testa, the tip of the seed invagination ends essentially in the center of the elongated cotyledons, unlike the situation in Cleomaceae, in which it touches the embryo near the base of the strictly incumbent, narrow cotyledons, and close to the transition to the elongated radicle-hypocotyl axis. Thus, the deeply invaginated, reniform seed of *Crateva* is a strong candidate as the plesiomorphic seed characteristic (Jacobs, 1960, 1964; Cornejo & Iltis, 2008a). Conversely, that its fat, irregularly incumbent cotyledons (Fig. 2A–D) do not lie horizontal and flat against each other as in Cleomaceae, but are variously and obliquely fitted one into the other, and with tips doubled and folded over each other and around the radicle as well, presages the typical, convoluted capparoid condition (Fig. 2E–H).

Eichler (1865: 239–242, 263–264, tab. 54–65) was evidently the first who appreciated these seed and embryo characteristics that distinguish Cleomaceae from Capparaceae. Within his all-inclusive Capparideae, he treated them as tribes distinguished by fruit type, cotyledons, and habit. Although these characters were not considered by Pax and Hoffmann (1936), Hutchinson (1967) emphasized the convoluted embryos and cotyledons of Capparaceae, which, except for the few but generally excellent seed illustrations in Eichler (e.g., 1865: tab. 64, figs. II 16, III 16), have rarely been adequately illustrated (Fig. 2A–H; Iltis, 1965: 60, fig. 2A–C; Iltis et al., 1996: 380, fig. 1D; Franceshini & Tressens, 2004: 213, figs. 4D–K, 5C; Iltis, Cochrane & Tucker, unpub.:

Figure 2. Continued. Seeds of *Tarenaya* Raf. (= *Cleome* sect. *Tarenaya* (Raf.) Iltis) revealing the large, empty, spherical cleft chamber closed at the cleft mouth, this evidently an adaptation for aquatic dispersal. —P. Seed of *T. hassleriana* (Chodat) Iltis (= *C. hassleriana* Chodat), a river margin and swamp species, commonly cultivated as *C. spinosa* Jacq. —Q, R. Seed of *C. trachycarpa* Klotzsch ex Eichler (from Iltis, 1967), another swamp species. —S, T. Seed of *C. torticarpa* Iltis & T. Ruíz (from Iltis & Ruiz-Zapata, 1997). —U–W. Seed of *Peritoma* DC. *Peritoma lutea* (Hook.) Raf. (= *C. lutea* Hook.), a species of arid grasslands and sands with conduplicate seeds and deep, narrow, tissue-filled seed clefts (from Iltis, 1950). X–Z. Seeds of Brassicaceae s. str.: *Stanleya pinnata* (Pursh) Britton (Ventura Co., California, *Bouquet s.n.* [WIS]), with a conduplicate-oblique embryo and a very short, nearly obsolete testa invagination between the radicle and inner cotyledon. Drawings by K. Elliot and H. H. Iltis (WIS).

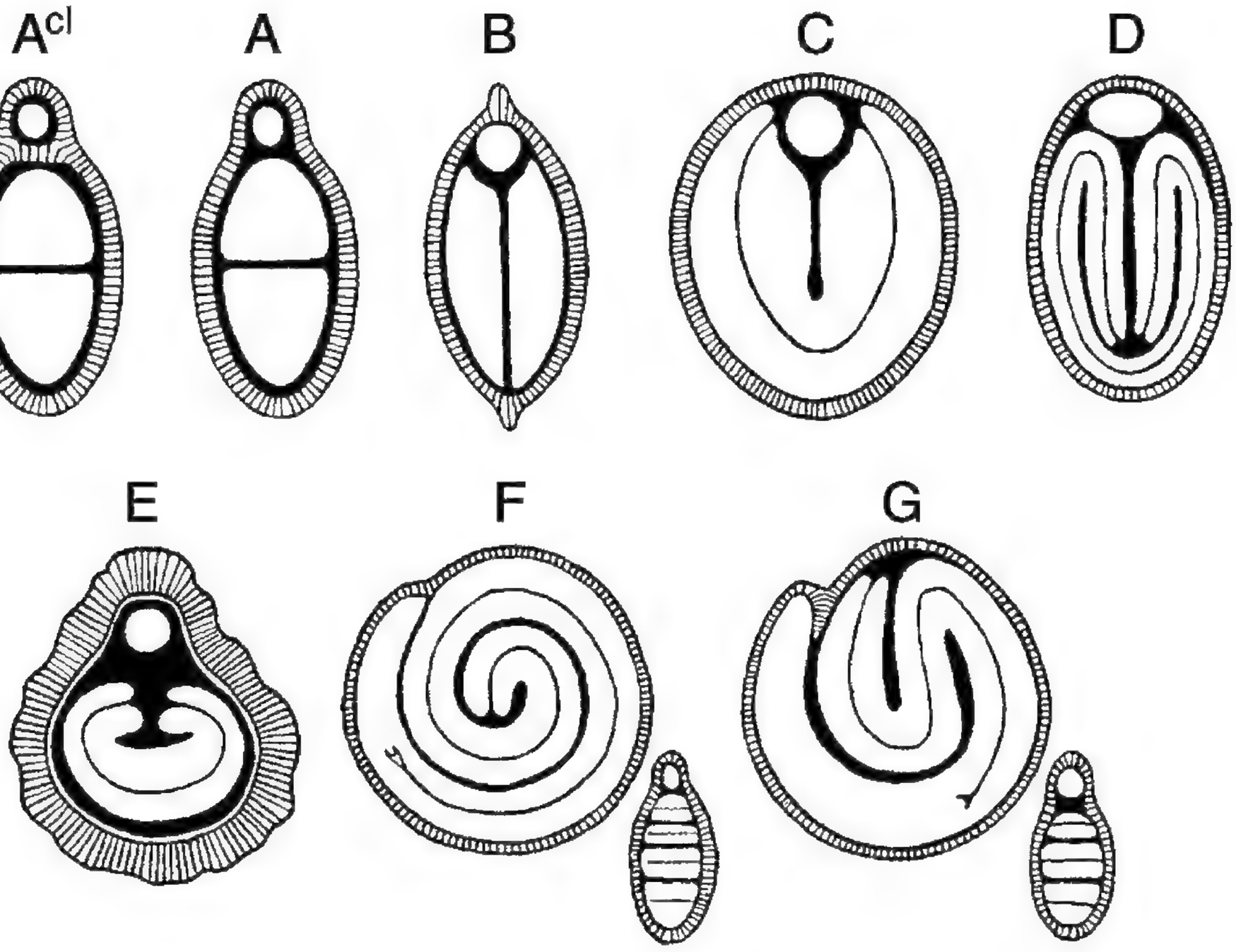

Figure 3. Seed morphology in Brassicales: configurations of embryo and testa. Cleomaceae (A^{cl}) and Brassicaceae (A–G), with testa indicated by short parallel lines. —A^{cl}. Cleomaceae, all species have uniformly incumbent cotyledons, e.g., *Tarenaya hassleriana* (Chodat) Iltis (= *Cleome hassleriana* Chodat) (cf. Fig. 2I–W, Cleomaceae; Fig. 2P, *T. hassleriana*; Iltis, Cochrane & Tucker, unpub.). A–G. Brassicaceae, showing the great diversity of embryo and testa configurations in this family, cf. Fig. 2X–Z. —A. *Sisymbrium strictissimum* L., with incumbent cotyledons. —B. *Cheiranthus cheiri* L., accumbent cotyledons. —C. *Brassica nigra* (L.) W. D. J. Koch, conduplicate cotyledons. —D. *Chamira circaeoides* (L. f.) Zahlbr., doubly conduplicate cotyledons. —E. *Calepina irregularis* (Asso) Thell., cross-folded cotyledons. —F. *Bunias erucago* L., spirolobous cotyledons. —G. *Heliophila pusilla* L. f., double cross-folded cotyledons. A^{cl}, from Iltis original drawing; A–G, adapted from diagrams in Melchior (1964: 184).

fig. 3). Clearly, much work remains to be done on utilizing these valuable yet cryptic, poorly understood, and variable characters of embryo and seed.

The mostly highly specialized seeds of Brassicaceae show remarkable variability in their cotyledonar and radicular configurations (Fig. 3A–G), yet some derived genera, like those of Cleomaceae (Fig. $3A^{cl}$), have a simple and incumbent or oblique conduplicate embryo (e.g., *Stanleya* Nutt., Fig. 2X–Z), in which the invagination of the testa in between the cotyledons and radicle is all but obsolete or very short (Fig. 2Y).

In conclusion, subsuming Capparaceae s.l., or even just the Cleomaceae, within an expanded Brassicaceae would obscure the many clear morphological characters that leave Brassicaceae a vast, yet practical, cohesive, and highly specialized family. The Cleomaceae constitute a distinct entity that is sister to Brassicaceae. Capparaceae, a more diverse family than Cleomaceae, lie sister to Brassicaceae plus Cleomaceae. This arrangement suggests that all three of these monophyletic clades should be recognized as independent families, lending powerful support to Airy Shaw's (1965: 256) conclusion that ". . .the recognition of the Cleomaceae is a logical necessity."

Key to the Capparaceae, Cleomaceae, and Brassicaceae

The following taxonomic key and family comparisons use mostly easily determined and visible characters, relying often on seed sectional views (Figs. 2–4), but do not delve into technical anatomical details of testa, exocarp or endocarp, or the fully mature fruit wall, which, while undoubtedly useful, cannot be dealt with easily by the closet taxonomist, who is faced with the almost hopeless task of resuscitating dried-out, squashed, fleshy fruits and juicy seeds glued-down together permanently onto herbarium sheets (cf. Kers, 2003, for references).

1a. Fruits with a false septum (rarely lacking, e.g., in *Pringlea* T. Anderson ex Hook. f.); stamens 6 (also 4 or 2 in *Lepidium* L., 10 to 16 in *Megacarpaea* DC.), most often tetradynamous (4 long, 2 short); seeds lacking a cleft or deep testa invagination between radicle and cotyledons; seeds small (0.5–2 mm); leaves not pulvinate ..... Brassicaceae

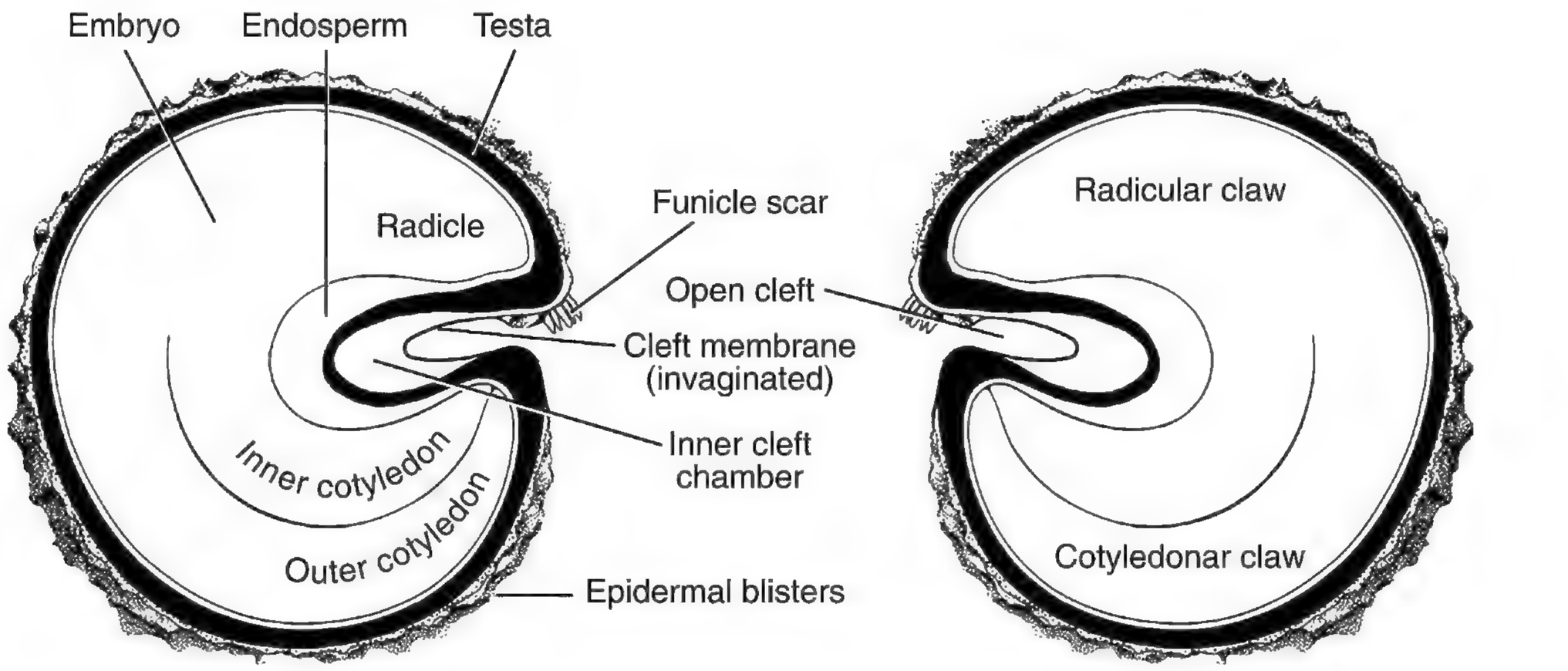

Figure 4. Cleomoid seed morphology: an illustrated glossary, based on *Cleome magnifica* Briq., as an example.

1b. Fruits lacking a false septum; stamens 1 to 250, not tetradynamous; seeds with or without a cleft or deep testa invagination between cotyledons and radicle; seeds small to large (0.5–30 mm); leaves often with pulvinate petioles 2

2a. Herbs, subshrubs, or rarely treelets; flowers often bracteate; leaves palmately compound, rarely unifoliolate or simple; fruits typically dry; seeds dry, small (0.5–4 mm), from either reniform or horseshoe-shaped to coiled or conduplicate, with the testa deeply invaginated between radicle and the narrow, semi-cylindric, always incumbent cotyledons, the radicle-hypocotyl elongate ..... Cleomaceae

2b. Trees or shrubs, rarely woody vines; flowers not noticeably bracteate; leaves simple or unifoliolate, rarely trifoliolate (*Crateva*); fruits fleshy and/or pulpy; seeds often surrounded by an aril or sarcotesta, large (5–30 mm), round to elongate, less often reniform or conduplicate (*Crateva*, some *Capparis* L. species), the testa often shallowly or not at all invaginated; cotyledons often foliaceous and green, usually convoluted or circinate, or cross-folded with each other, sometimes white and greatly thickened, mostly incumbent to accumbent, the radicle-hypocotyl axis short and conical ..... Capparaceae

Comparative Descriptions of Brassicaceae, Cleomaceae, and Capparaceae

Brassicaceae Burnett, Outl. Bot. 854, 1093, 1123. 1835, nom. cons. (cf. ICBN, App. IIB; McNeill et al., 2006: 140) TYPE: *Brassica* L.

Plants annual, biennial, to perennial herbs, rarely shrubby and woody; indument diverse, the hairs often malpighian, branched or stellate; mostly in cold to warm, often xeric temperate climates. *Leaves* simple, sessile, alternate, rarely opposite, sometimes pinnately dissected, lacking both stipules and pulvinus. *Flowers* usually in dense bractless racemes, generally actinomorphic and with small, white, yellow, or purple petals; stamens nearly uniformly 6 and tetradynamous, never forming an androgynophore; ovaries and fruits usually sessile, in a few genera (e.g., *Romanschulzia* O. E. Schulz, *Stanleya*) borne on a slender gynophore. *Fruits* dry elongate siliques to short and round capsules or silicles, variable in structure and dehiscence, the valves usually deciduous from a persistent replum that encircles a thin, translucent partition (false septum) dividing the fruit into 2 locules, or the valves (or parts thereof) persisting around a seed and falling as one unit, or seeds falling freely or permanently enclosed in parts of the fruit wall. *Seeds* (Figs. 2X–Z, 3A–G) small, mostly 0.5–2 mm diam.; testa smooth or variously ornamented, in longitudinal section usually not invaginated between cotyledons and radicle; *embryo* (Figs. 2X–Z, 3A–G) basically incumbent or accumbent (these two types nearly equally distributed in the family), variable, with the small, white cotyledons more often in diverse configurations, commonly lying against the radicle; *germination* always epigeal.

(For recent comprehensive references on the Brassicaceae, see Appel & Al-Shehbaz, 2002; Koch et al., 2003; Al-Shehbaz et al., 2006; Koch & Mummenhoff, 2006.)

Cleomaceae Horan., Prim. Lin. Syst. Nat. 92. 1834. [Isonym: Cleomaceae Airy Shaw, Kew Bull. 18(2): 256. 1965.] TYPE: *Cleome* L.

Plants annual or perennial herbs, often giant herbs or subshrubs, rarely woody shrubs to treelets; indument various, the hairs unicellular, uniseriate; mostly warm-temperate to tropical, arid desert or grasslands to humid, forested environments. *Leaves* alternate, petiolate and palmately compound, 3- to 11-foliolate, rarely sessile and/or unifoliolate (particularly in

specialized taxa), thin and deciduous, rarely with minute, marcescent stipules, sometimes with stipular but hair-derived thorns, pulvinate or epulvinate, entire or minutely serrulate. *Flowers* in bracteate or less often ebracteate racemes, or rarely singly in the axils of leaves, zygomorphic to actinomorphic, 4-merous, often pink to purple, or yellow to white or dull greenish, generally day-, evening-, or night-bloomers; stamens 6 to 27(to 110) or by sterilization of the basic 6 reduced to 4, 2, or 1 fertile and 1 to 5 staminodes (or 6 staminodes, i.e., functionally pistillate flowers in *Podandrogyne* Ducke), equal or of variable lengths, sometimes adnate for part of their length to the gynophore, forming an androgynophore; ovaries usually borne on a gynophore or sessile. *Fruits* dry, elongate to short, round capsules, the 2 valves freely dehiscing from a thin (thick in *Podandrogyne*), hooplike or framelike replum lacking a false septum; or, less often, dehiscing partway from the top but remaining basally fused to the replum and receptacle; or, very rarely (*Oxystylis* Torr. & Frém., *Wislizenia* Engelm.), valves each permanently enclosing and dehiscing with their 1 to 2(to 3) seeds. *Seeds* (Figs. 2I–W, 3A[cl], 4) small, 0.5–3(–4) mm, strongly incurved, from either reniform or horseshoe-shaped to coiled or conduplicate, the two arms or claws of the seed free to the vertex (Fig. 4) to totally, or the basal half only, fused from without by an external cleft membrane, forming in longitudinal section a spherical and hollow, to narrow and wedgelike, or solid, closed, and obsolete, cleft chamber; seeds dry or, if carunculate, equipped with oil-filled cells or a white funicular aril and presumably dispersed by ants; testa dry, smooth to transverse-rugose or tubercled, glabrous or pubescent to variously ornamented. *Embryo* (Figs. 2I–W, 3A[cl]; Iltis, Cochrane & Tucker, unpub., figs. 1, 2) uniformly incumbent, with the semicylindric, narrow, straight cotyledons flat on top of each other, with the back of the inner cotyledon facing the radicle but separated from it by the deep cleft of the invaginating testa. *Germination* epigeal, the cotyledons in the seeds small, white, and not expanding into wide, green leaves. Seed viability variable, from short to many years.

Capparaceae Juss., Gen. Pl.: 62. 1789, nom. cons. (cf. ICBN, App. IIB; McNeill et al., 2006: 141). TYPE: *Capparis* L.

Plants shrubs to treelets to trees, sometimes scramblers, rarely (in the New World) lianas; indument various, the hairs unicellular, stellate or peltate; mostly subtropical to tropical, from dry to moist environments. *Leaves* usually alternate, distichous to spiral and clustered, simple or unifoliolate and pulvinate, petiolate to subsessile, rarely palmately trifoliolate (*Crateva*), often evergreen, entire. *Flowers* mostly in ebracteate, often corymbiform racemes or solitary in axils of leaves, actinomorphic to rarely zygomorphic, 4-merous, white or greenish to purplish white, usually night-blooming; stamens (1 to)8 to 250 (rarely 6), ± equal; ovaries mostly borne on gynophores, rarely sessile. *Fruits* either dehiscent, 2-carpellate, fleshy (rarely tardily dry), elongate capsules lacking a false septum or baccate with repla (the parietal placentae) mostly thin, the valves often tardily dehiscing or repla obscure or in indehiscent berries obsolete, lacking a false septum but sometimes with endocarp intrusions and then axile placentation. *Seeds* large, 5–15(–30) mm, spherical to ovoid or ellipsoid, straight or broadly incurved to reniform-conduplicate; testa smooth, thick and hard to very thin, slippery and easily removed, often covered by a fleshy-oily, funicular aril or by a hair-infiltrated sarcotesta (Fig. 2A–H), or immersed in the red, orange, or cream to white endocarp pulp; testa often shallowly or not at all invaginated into the embryo (deeply so in *Crateva*, *Capparis* spp.), the two claws of the seed not conjoined by distinct cleft membranes (Fig. 2A–H); *embryo* green to ivory-white, variable, mostly conduplicate, with cotyledons incumbent or accumbent, but often foliaceous, much enlarged and variously convoluted one inside the other and sometimes around the radicle (Fig. 2A–H); *germination* epigeal, the cotyledons often large, green, and leaflike, or sometimes ivory or white and very thick and food-storing, rarely quite unequal with one suppressed.

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REVISION OF THE INFRAGENERIC CLASSIFICATION OF *LOBELIA* L. (CAMPANULACEAE: LOBELIOIDEAE)

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Abstract

The infrageneric classification of the cosmopolitan genus *Lobelia* L. (Campanulaceae) is revised via synthesis of diverse phenotypic data. The 415 species are divided among 18 sections (numbers of included species are given in parentheses): *Lobelia* sect. *Delostemon* (E. Wimm.) J. Murata (44); *Lobelia* sect. *Holopogon* Benth. (14); *Lobelia* sect. *Colensoa* (Hook. f.) J. Murata (1); *Lobelia* sect. *Cryptostemon* (E. Wimm.) J. Murata (10); *Lobelia* sect. *Stenotium* (C. Presl) Lammers (144); *Lobelia* sect. *Lobelia* (22); *Lobelia* sect. *Hypsela* (C. Presl) Lammers (43); *Lobelia* sect. *Mezleriopsis* Lammers, sect. nov. (7); *Lobelia* sect. *Jasionopsis* Lammers, sect. nov. (1); *Lobelia* sect. *Tylomium* (C. Presl) Benth. (38); *Lobelia* sect. *Homochilus* A. DC. (5); *Lobelia* sect. *Tupa* (G. Don) Benth. (4); *Lobelia* sect. *Trimeris* (C. Presl) A. DC. (1); *Lobelia* sect. *Speirema* (Hook. f. & Thomson) Lammers (5); *Lobelia* sect. *Plagiobotrys* Lammers (1); *Lobelia* sect. *Rhynchopetalum* (Fresen.) Benth. (61); *Lobelia* sect. *Revolutella* E. Wimm. (9); and *Lobelia* sect. *Galeatella* E. Wimm. (5). In addition, *Monopsis* Salisb. sect. *Xanthomeria* (C. Presl) Lammers, comb. nov., is validated to provide the correct name for *Monopsis* sect. *Parastranthus* (G. Don) E. Wimm.

Key words: Campanulaceae, classification, *Hypsela*, infrageneric, *Isotoma*, *Lobelia*, Lobelioideae, *Monopsis*, nomenclature, *Pratia*, typification.

"This whole genus would richly reward any botanist for an analytical investigation."

—Lindley (1826)

Large polytypic genera pose special problems for taxonomists. To simply place 200 or more species into a genus without some indication of relationships among them is most unsatisfying. We know that all of these species did not radiate simultaneously from some ancestor; we know that some will have more character states in common with one another than they will have with other congeners. In order to convey our understanding of these relationships and similarities, additional taxonomic structure is required (Stuessy, 2009).

Lobelia L. is a perfect example. With 415 species (Argent et al., 2007; Lammers, 2007a, 2007b; Heenan et al., 2008; Knox et al., 2008a; Senterre & Castillo-Campos, 2008), it is the second largest of the 84 genera in Campanulaceae Juss. and the largest of the 29 genera in subfamily Lobelioideae Burnett (Lammers, 2007a). Its members are extremely diverse in growth form, habit, reproductive strategies, floral structure and color, pollination syndromes, fruit type, seed morphology, and chromosome number (Lammers, 2007c).

Some believe that science is best served by dividing polytypic genera into smaller, more homogeneous genera, particularly when the genus is a "residual concept" rather than an explicitly diagnosed taxon (King & Robinson, 1987). Irrespective of the merits of this approach, I hesitate to follow it at this time because of the heavy cost it exacts due to our binomial system of species nomenclature. Each change in generic assignment means that a new binomial must be coined or an old one resurrected. This creates confusion for users of our classifications as well as increased workloads for those who index nomenclatural novelties and maintain electronic databases. Applying this approach to *Lobelia* would result in as many as 393 of the 415 recognized species taking a different and, in most cases, new binomial (Lammers, 2007a). Furthermore, dismemberment of *Lobelia* would be premature. At least three laboratories (Koopman & Ayers, 2005; Knox et al., 2006, 2008a, 2008b; Antonelli, 2008) are actively generating DNA sequence data that would be extremely useful in such an undertaking; however, these studies are as yet rather preliminary; large pieces of lobelioid diversity have yet to be included. If the world must be inconvenienced by the appearance of nearly 400 unfamiliar names, it should

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only be done on the soundest evidentiary basis possible.

Nonetheless, there is a very real need for a revision of the existing classification of *Lobelia*. The two classifications in current use (Wimmer, 1943, 1953, 1968; Murata, 1995) each have serious shortcomings. The former is based on too few (often single) characters and features a confusing multiplicity of ranks and unranked taxa. The latter is a marked improvement, far more holistic and synthetic in its use of characters and far simpler in structure. However, it does not assign every species to a taxon, instead merely listing exemplars for each. More seriously, some names in both classifications violate the *International Code of Botanical Nomenclature* (ICBN; McNeill et al., 2006).

As noted above, a wealth of molecular data pertinent to this genus is on the horizon. New data such as this can be used to test an existing classification in the same way that the results of an experiment can be used to test a hypothesis (Cracraft, 1978; Gilmartin, 1986; Donoghue, 1987; LaDuke, 1987). To do so, however, the existing classification must be sound, representing a synthesis of all available data. As this is not the case for *Lobelia*, a revised classification is promulgated here. At the very least, its availability will keep those crafting the next classification from falling prey to the incompleteness and nomenclatural mistakes that plagued earlier efforts.

Taxonomic History

The generic name *Lobelia* originated with Plumier (1703), who coined the polynomial *L. frutescens, portulacae folia* for the littoral shrub known today as *Scaevola plumieri* (L.) Vahl (Goodeniaceae). Linnaeus (1753, 1754) took up this generic name (giving the original species the binomial *L. plumieri* L.), but added to it numerous species today assigned to Campanulaceae, which had been assigned by pre-Linnaean authors to the genera *Dortmanna* O. O. Rudbeck ex Hill, *Laurentia* Adans., and *Rapuntium* Mill. As such, Linnaeus's *Lobelia* was at a minimum biphyletic, incorporating species of two disparate families.

Various contemporaries (e.g., Miller, 1754, 1768; Adanson, 1763) objected to this broad circumscription and restricted *Lobelia* to the original goodeniaceous species, resurrecting various pre-Linnaean generic names for the campanulaceous interlopers. Miller (1754) thereby created a later homonym of the Linnaean *Lobelia*. A second later homonym was created by Presl (1836) when he inexplicably excluded all of the original Linnaean species from *Lobelia* and left only species described later, the majority assigned today to *Siphocampylus* Pohl; for *Lobelia* in the Linnaean sense, he used the name *Rapuntium*.

Eventually, Linnaeus (1771) admitted that his circumscription was unnatural. However, rather than render *Lobelia* goodeniaceous, as others had done, he segregated *L. plumieri* as a new genus, *Scaevola* L., thereby creating a thoroughly campanulaceous *Lobelia*. De Candolle's (1839) endorsement of this action ensured its acceptance by all but a handful of recalcitrants (e.g., Kuntze, 1891, 1898; Post & Kuntze, 1903; Safford, 1905).

The first to promulgate an infrageneric classification of the genus was Presl (1836), who divided his *Rapuntium* into *Rapuntium* sect. *Xanthomeria* C. Presl, *Rapuntium* sect. *Stenotium* C. Presl, and *Rapuntium* sect. *Sphaerangium* C. Presl. Endlicher's (1838) classification of *Lobelia* was identical except for his failure to indicate the rank of his infrageneric taxa (Brizicky, 1969) and the segregation of *L. dortmanna* L. as a fourth taxon. De Candolle (1839) removed *Rapuntium* sect. *Xanthomeria* from *Lobelia* as the genus *Parastranthus* G. Don. The two remaining Preslian sections he largely combined as *Lobelia* sect. *Rapuntium* (Mill.) A. DC., though a few species of *Rapuntium* sect. *Sphaerangium* were segregated as *Lobelia* sect. *Homochilus* A. DC.; the monotypic genus *Trimeris* C. Presl was subsumed as a third section. Heynhold (1840) created 11 unranked infrageneric taxa in *Lobelia* by subordinating previously recognized genera (*Centropogon* C. Presl, *Dobrowskya* C. Presl, *Enchysia* C. Presl, *Isolobus* A. DC., *Laurentia*, *Monopsis* Salisb., *Parastranthus*, *Piddingtonia* A. DC., *Pratia* Gaudich., *Siphocampylus*, and *Tupa* G. Don). His twelfth taxon, representing *Lobelia* in the sense of Endlicher (1838) and de Candolle (1839), was denoted as "*Lobelia genuina*."

Bentham's (1876) treatment likewise featured an expanded circumscription, though not so broad as Heynhold's (1840). The three sections of de Candolle (1839) were retained (with *Lobelia* sect. *Rapuntium* renamed *Lobelia* sect. *Eulobelia* Benth.). Two sections erected by Bentham previously (*Lobelia* sect. *Hemipogon* Benth. and *Lobelia* sect. *Holopogon* Benth.) and three genera recognized by earlier authors (creating *Lobelia* sect. *Tupa* (G. Don.) Benth., *Lobelia* sect. *Tylomium* (C. Presl) Benth., and *Lobelia* sect. *Rhynchopetalum* (Fresen.) Benth.) were added to this. Schönland's (1889) classification was very similar, with the addition of two more former genera as *Lobelia* sect. *Mezleria* (C. Presl)

Schönl. and *Lobelia* sect. *Isolobus* (A. DC.) C. B. Clarke, and the merger of *Lobelia* sect. *Tylomium* and *Lobelia* sect. *Rhynchopetalum* under the former name.

Like Presl (1836), Post and Kuntze (1903) insisted that *Rapuntium* was the correct name for the genus. Their classification differed from that of Schönland (1889) in the segregation of *Rapuntium* sect. *Trematocarpus* Kuntze from *Rapuntium* sect. *Tupa* (G. Don) Kuntze, and *Rapuntium* sect. *Haynaldia* Kuntze from *Rapuntium* sect. *Tylomium* (C. Presl) Kuntze; inclusion of the genera *Grammatotheca* C. Presl, *Monopsis*, and *Parastranthus* as sections; and the renaming of *Lobelia* sect. *Eulobelia* and *Lobelia* sect. *Hemipogon* as *Rapuntium* sect. *Cardinalis* Kuntze and *Rapuntium* sect. *Dortmanna* (O. O. Rudbeck ex Hill) Kuntze, respectively.

The most highly structured classification of *Lobelia* was that of Wimmer (1943, 1953, 1968), which was derived from Schönland's (1889) and was the first since de Candolle (1839) to assign every recognized species to an infrageneric taxon. A major innovation was the apportionment of the sections among three subgenera: *Lobelia* subg. *Lagotis* E. Wimm. (later corrected to *Lobelia* subg. *Lobelia*), *Lobelia* subg. *Mezleria* (C. Presl) E. Wimm., and *Lobelia* subg. *Tupa* (G. Don) E. Wimm. *Lobelia* subg. *Lobelia* comprised two sections, *Lobelia* sect. *Hemipogon* (later corrected to *Lobelia* sect. *Lobelia*) and *Lobelia* sect. *Holopogon*. The former was divided into *Lobelia* subsect. *Trachyspermae* E. Wimm. (which should have been corrected to *Lobelia* subsect. *Lobelia*) and *Lobelia* subsect. *Leiospermae* E. Wimm., the latter into *Lobelia* subsect. *Cryptostemon* E. Wimm. and *Lobelia* subsect. *Delostemon* E. Wimm. *Lobelia* subg. *Mezleria* likewise comprised two sections, *Lobelia* sect. *Eumezleria* E. Wimm. (later corrected to *Lobelia* sect. *Mezleria*) and *Lobelia* sect. *Paramezleria* E. Wimm. *Lobelia* subg. *Tupa* comprised six sections: *Lobelia* sect. *Isolobus*, *Lobelia* sect. *Eutupa* A. DC. ex E. Wimm. (later corrected to *Lobelia* sect. *Tupa*), *Lobelia* sect. *Rhynchopetalum*, *Lobelia* sect. *Homochilus*, *Lobelia* sect. *Revolutella* E. Wimm., and *Lobelia* sect. *Galeatella* E. Wimm.; of these, *Lobelia* sect. *Tupa* was divided into *Lobelia* subsect. *Primanae* E. Wimm. and *Lobelia* subsect. *Haynaldianae* E. Wimm. Some of the subsections were divided into greges and subgreges. Wimmer also used the symbol "§" to denote "kleinere Gruppen (ohne Rang)" (1953: 479), in one case within a grex, in others within a subsection.

Many of the taxa in Wimmer's (1943, 1953, 1968) classification were defined by single characters. For example, *Lobelia* subg. *Lobelia* and *Lobelia* subg. *Mezleria* were distinguished from *Lobelia* subg. *Tupa* solely on habit: "saepe annuae, debilies vel fruticuli graciles" in the former versus "robustae, suffrutices vel frutices" in the latter (with the proviso that *Lobelia* subg. *Tupa* sect. *Isolobus* actually resembled the other two subgenera in habit). Similarly, *Lobelia* sect. *Holopogon* and *Lobelia* sect. *Lobelia* were distinguished solely on the basis of whether all five or only the ventral pair of anthers were bearded at the apex. One's confidence in the naturalness of a classification that embodies this sort of single-feature characterization is frankly quite low.

In this regard, the classification of Murata (1995) represented a marked improvement because of his attempt to find multiple correlations among functionally unrelated characters (cf. Stuessy, 2009). Specific changes were: (1) narrowing the circumscription of *Lobelia* sect. *Lobelia* so that it encompassed only *Lobelia* subsect. *Lobelia*; (2) removal of *Lobelia* subsect. *Leiospermae* from *Lobelia* sect. *Lobelia* and recognition of most of it as *Lobelia* sect. *Heyneana* J. Murata; (3) treatment of the remainder of *Lobelia* subsect. *Leiospermae* as *Lobelia* sect. *Dioicae* (E. Wimm.) J. Murata in *Lobelia* subg. *Mezleria*; (4) division of *Lobelia* sect. *Holopogon* into *Lobelia* sect. *Cryptostemon* (E. Wimm.) J. Murata and *Lobelia* sect. *Delostemon* (E. Wimm.) J. Murata; (5) addition of *Pratia* sect. *Pratia* to *Lobelia* sect. *Mezleria* (which thus became *Lobelia* sect. *Pratia* (Gaudich.) J. Murata); (6) placement of *Lobelia* sect. *Isolobus* in *Lobelia* subg. *Mezleria* instead of *Lobelia* subg. *Tupa*; (7) addition of *Pratia* sect. *Colensoa* (Hook. f.) Baill. to *Lobelia* subg. *Tupa* as *Lobelia* sect. *Colensoa* (Hook. f.) J. Murata; and (8) removal of all non-Chilean species of *Lobelia* sect. *Tupa* to *Lobelia* sect. *Colensoa*. No ranks lower than section were used.

Despite its improvements, there were still shortcomings. Only types and a few other exemplars were assigned to each section; one is left to guess where the remainder belong. (This is complicated by the fact that a few exemplars were said to belong to one section in the text and a different one in the accompanying table.) Additionally, some of the names used violate provisions of the ICBN. For example, at sectional rank *Hemipogon* has priority over *Pratia*, while *Stenotium* and *Microcentron* have priority over *Heyneana*.

Characters and Their States

Phenotypic traits of the Campanulaceae have been described in detail by Lammers (2007c). In this

section, some of the more complex characters that have proven particularly efficacious in crafting the revised classification of *Lobelia* are explained and discussed, to ensure that the descriptions provided below are understood fully.

HABIT

Lobelia is extremely heterogeneous in overall body plan, more so than any other genus in the family. First, the various species form a continuum from fully herbaceous plants that undergo no secondary growth or lignification, to those that become lignified in their basal portions, to those that amass considerable wood throughout their axes, building trees up to 9 m tall.

Second, relative stoutness of the stems varies considerably, irrespective of the presence or absence of lignification. In many species, the stems are no more than 5 mm in diameter, even when some secondary growth takes place; such stems are here termed gracile. Stems of greater girth, which often are woody to some degree, are termed robust. Very robust stems with a broad parenchymatous or hollow pith are termed pachycaul (the gracile and less robust stems are contrasted as leptocaul).

Third, the longevity of individual plants varies. Most species, whether herbaceous or woody, are iteroparous (polycarpic). Among species that are semelparous (monocarpic), those with gracile stems are typically annual or in a few cases biennial, while those with robust and especially pachycaul stems are pliestesial.

Fourth, almost every life form (Raunkiaer, 1934) is represented. Hemicryptophytes are perhaps the commonest, followed by geophytes and chamaephytes; these all may be considered "herbaceous perennials." The remaining herbaceous species are therophytes. Woody plants include both nanophanerophytes (subshrubs, shrubs, and treelets) and phanerophytes (large shrubs and trees). Most species are terrestrial, but a few are facultatively or obligately hydrophytic.

INFLORESCENCE

The basic reproductive unit in *Lobelia* is a solitary pedicellate flower in the axil of a leaf, typically a leaf near the apex of the stem. The pedicel frequently bears a pair of opposite or subopposite bracteoles, typically in the proximal two thirds; in many species, however, these are altogether lacking.

When multiple flowers are produced (by far the norm), the sequence of bloom is always acropetal (centripetal). The stem is characteristically anauxotelic, i.e., incapable of resuming vegetative growth after flowering ceases. If the leaves that subtend the flowers differ in neither size nor shape from ordinary foliage, the plants are said to bear solitary axillary flowers. More commonly, these distal floral leaves are smaller and shaped differently from the foliage below, i.e., they are bracts. As a result, the flowers are borne in a terminal raceme.

Sometimes, the transition from foliage to bracts is very gradual; such "foliose racemes" may be mistaken for a stem with solitary axillary flowers, particularly when anthesis begins. Other times, the change from foliage to bracts is quite abrupt and a distinct peduncle may separate the distalmost leaf from the basal bract. In such "bracteate racemes," the demarcation of the inflorescence is quite obvious. Variation in pedicel length can cause a raceme to resemble a spike (uniformly short pedicels), a corymb (pedicel length decreasing acropetally), or an umbel (rachis condensed). In some species, branches arise near the base of the raceme, creating a panicle. In two species, the bracteate racemes become pseudoaxillary via sympodial growth, i.e., though terminal, they are soon overtopped by vegetative growth from an adjacent axillary bud.

COROLLA

As with habit, the appearance of the corolla varies enormously. First, the five lobes may all be relatively uniform in size, shape, and connation, i.e., monomorphic. Alternatively, the three ventral lobes may be larger, broader, and connate for a greater distance than the dorsal pair, i.e., the lobes are dimorphic. In one small group of the latter, however, the central ventral lobe is conspicuously larger and wider than the two flanking it.

Second, angular orientation of the lobes around the flower's axis varies; this is best understood by mentally superimposing a clockface on the flower as seen in face view. In species with dimorphic lobes, the corolla is bilabiate: the two dorsal lobes more or less parallel one another in an upright posture, while the ventral three spread out as a trifid lip. In other words, the dorsal lobes are oriented at 12 o'clock or at 11 and 1 o'clock, while the ventral lobes fall at 4, 6, and 8 o'clock. In species with monomorphic lobes, greater variation is possible. Some species have a bilabiate corolla as described above, though the distinction between the dorsal and ventral lip may not be as pronounced as it is when the lobes are dimorphic. Far more common is for the dorsal lobes to arise in a slightly more ventral

position, e.g., at 10 and 2 o'clock, making the symmetry appear more radial than bilateral; this type of corolla is here termed sub-bilabiate. Some bilabiate or sub-bilabiate corollas feature a distinct palate or a pair of variously prominent gibbosities on the ventral lobes at their mouth. Finally, all five lobes may be displaced ventrally in a single plane, i.e., they all fall between 4 and 8 o'clock; this is termed a unilabiate corolla.

Third, the connate portion of the petals (the corolla tube) varies in several features. The tube may be straight or nearly so, or curved ventrally to a greater or lesser extent. When straight or nearly so, the axis of the corolla tube typically forms a line with the axis of the hypanthium; in one small group, however, the former is deflected ventrally at an acute angle from the latter. In nearly all members of the genus, the dorsal side is cleft from its mouth almost to its base; in a few species, this cleft only extends partway to the base or is entirely absent. In some species, small window-like openings (fenestrations) develop laterally toward the base. In other species, a slender long or short nectar spur develops at the base of the corolla tube; this distorts the hypanthium, displacing the ventral pair of calyx lobes to the distal end of the spur.

Fourth, the proportion of the petal that is connate varies. The three ventral petals may be more connate than the dorsal pair, or all five petals may be equally connate, forming lobes of approximately the same length. The former condition is typically expressed as a trifid ventral lip and a pair of dorsal lobes that are separate from it for about half their length. In a few species, the dorsal pair is separate from the ventral lip for nearly its entire length. In the case of petals that are more or less equally connate throughout, they may be fused for half their length or less, forming lobes about as long as the tube or longer; or for more than three quarters of their length, forming lobes that are one quarter as long as the tube or less.

Finally, there is a great deal of variation in the pigmentation of the corolla. Most species are some shade of blue or purple, often with undertones of rose or mauve, though hues from the opposite end of the spectrum are common, including red, pink, magenta, orange, and yellow. Chlorophyllous (green) corollas are more common than one might suppose in a genus with conspicuous zygomorphic sympetalous flowers. Unpigmented (white) corollas are not uncommon, both as the norm for a species and as occasional mutants in species with pigmented flowers. Corollas showing two or even three colors are not uncommon. Common patterns are blue or purple with white and/or yellow at the mouth, and a red tube with yellow and/or orange lobes.

ANTHERS

Lobelioideae possess a specialized method of proterandrous secondary pollen presentation (Erbar & Leins, 1989, 1995; Leins & Erbar, 1990). An important component of this is the trichomes at the orifice of the ventrally oblique anther tube, which function as a lever for the discharge of pollen. In many species, the apices of the anthers are bearded with tufts of hairs, either on all five anthers or just the ventral pair. These hairs are filiform, except in one species where they are flattened. In some species, a single long narrowly triangular flattened or awnlike bristle adorns the apex of each ventral anther; this is sometimes supplemented by a tuft of filiform hairs. In a few species, the orifice of the anther tube is nude, with neither hairs nor bristles.

SEEDS

Murata (1992) studied in detail the morphology of the seed coat (testa) in Lobelioideae and relied heavily on these data in crafting his classification of *Lobelia* (Murata, 1995). Five distinct patterns were recognized; only the surface aspects are summarized here, although each type is also characterized by distinctive features of its internal structure. The testa of type A seeds is reticulate, with the cells longer than wide and the radial walls irregularly elevated above its surface, giving the seed a roughened appearance. The testa of type B seeds is also reticulate, but the cells are more or less isodiametric and the walls project but slightly; these seeds are sometimes said to have a pitted appearance. Type E seeds are identical except for the lack of a cuticle. The testa of type C seeds is likewise reticulate with less prominent cell walls, but the cells are so elongate (even more so than in type A) that such seeds are often described as striate-reticulate in appearance. In type D seeds, the cells have become so elongate that they are very difficult to recognize; the overall appearance is striate or almost smooth.

In addition to testal patterns, seeds in *Lobelia* vary in shape as seen in transverse section; the commonest cross section is terete or nearly so; some of these become rather irregularly angular, cuboidal, or quadrate. A significant number of species have distinctly trigonous seeds, while others are strongly compressed (lenticular); the last in many cases

develop a partial or complete wing around the circumference.

CHROMOSOME NUMBER

Published chromosome numbers for *Lobelia* were summarized and discussed by Lammers (1993); additions have been made by several authors (Knox & Kowal, 1993; Stace & James, 1996; Ruas et al., 2001; Murray et al., 2004) and a few overlooked counts discovered (Lepper, 1979, 1980, 1982). The base chromosome number (x) for *Lobelia* is readily interpreted as seven, making the numerous plants with $2n = 14$ diploid. From this base, several levels of polyploidy have evolved, including tetraploid ($2n = 28$), hexaploid ($2n = 42$), octoploid ($2n = 56$), decaploid ($2n = 70$), endecaploid ($2n = 77$), dodecaploid ($2n = 84$), tridecaploid ($2n = 91$), and icosaploid ($2n = 140$). Additional numbers ($2n = 12$, 16, 18, 20, 22, 24, 26, 38) are interpreted as aneuploid, although allopolyploidy cannot be ruled out.

TAXONOMIC TREATMENT

Only those names validated by citing *Lobelia* as a synonym are listed as synonyms of the generic name per se. All other effectively published supraspecific names referable to the genus will be found under the section to which its type belongs. This includes the following names at generic rank: *Calcaratolobelia* Wilbur, *Colensoa* Hook. f., *Dortmanna*, *Enchysia*, *Euhaynaldia* Borbás, *Galeatella* (E. Wimm.) O. Deg. & I. Deg., *Haynaldia* Kanitz, *Holostigma* G. Don, *Holostigmateia* Rchb., *Hypsela* C. Presl, *Isolobus*, *Neowimmeria* O. Deg. & I. Deg., *Petromarula* Belli ex Nieuwl. & Lunell, *Piddingtonia*, *Pratia*, *Rapuntium*, *Rhynchopetalum* Fresen., *Speirema* Hook. f. & Thomson, *Trimeris*, *Tupa*, and *Tylomium* C. Presl. An index to sectional assignments for all species included within *Lobelia* by Lammers (2007a) is provided in Appendix 1.

Lobelia L., Sp. Pl. 2: 929. 1753. *Cardinalis* Riv. ex Fabr., Enum. 122. 1759, nom. illeg. sub Art. 52.1. *Laurentia* Adans., Fam. Pl. 2: 134, 568. 1763, nom. illeg. sub Art. 52.1 (Brummitt, 2000; but cf. Lammers, 1997). *Mecoschistum* Dulac, Fl. Hautes-Pyrénées 459. 1867, nom. illeg. sub Art. 52.1. TYPE [designated by Hitchcock & M. L. Green in Anon., Nomencl. Prop. Brit. Bot. 184. 1929]: *Lobelia cardinalis* L. [Under Art. 10.5(b), this supercedes the earlier choice of *Lobelia dortmanna* L. (Ill. Fl. N. U.S. (Britton & Brown) 3: 29. 1913) (cf. McNeill et al., 1987).]

Plants perennial (hemicryptophytes, geophytes, chamaephytes, nanophanerophytes, or phanerophytes) or annual (rarely biennial), sometimes pliestesial, 0.02–9 m tall, terrestrial or rarely hydrophytic or epiphytic. Roots fibrous or rarely tuberous, adventitious or the primary root persisting as a tap root. Stems gracile or robust, the latter sometimes pachycaul, herbaceous, suffruticose, or woody, prostrate, decumbent, ascending, or erect, simple to much branched, sometimes rhizomatous, stoloniferous, and/or apically or basally rosulate; latex acrid, viscous, white or rarely colored. Leaves alternate, simple, exstipulate, dillenid, dorsiventral (rarely centric), pinnately (rarely palmately) veined, sessile or petiolate; margin commonly variously toothed, less often entire, rarely lobed or parted. Flowers tetracyclic, perfect (rarely imperfect and the plants then dioecious or gynodioecious), zoophilous, chasmogamous with a specialized method of protandrous secondary pollen presentation, resupinate, epigynous, zygomorphic, pedicellate, solitary in the axils of the upper leaves or these reduced in size, creating a terminal (very rarely pseudoaxillary) foliose or bracteate anauxotelic (very rarely auxotelic) raceme, sometimes branching (paniculate), rarely spikelike, corymbose, or subumbellate in appearance; pedicels bibracteolate or ebracteolate, very rarely oligobracteolate. Calyx synsepalous, radially (rarely bilaterally) symmetric, adnate to the ovary, forming an appendicular hypanthium; lobes 5 (very rarely 4), valvate, typically triangular, rarely with a reflexed auriculate appendage in each sinus. Corolla early-sympetalous, typically for half or more of its length, bilaterally (rarely almost radially) symmetric, bilabiate or sub-bilabiate with 2 dorsal and 3 ventral lobes or unilabiate with 5 ventral lobes, typically some shade of blue or purple, often with undertones of rose or mauve, less often red, pink, magenta, orange, yellow, green, or white, concolorous or subtly (less often sharply) bicolorous or tricolorous, very rarely with a slender long or short ventral nectar spur; tube straight to arcuate, typically cleft almost to its base on the dorsal side, rarely only partway or even entire, sometimes laterally fenestrate; lobes valvate, monomorphic, or dimorphic with the ventral 3 larger, sometimes with a palate or a pair of gibbosities on the ventral lip at the mouth of the tube. Stamens 5, antisepalous, inserted on rim of hypanthium or at very base of corolla tube, connate distally, forming an exserted (rarely included) and dorsally deflected staminal column free from (rarely adnate to) the corolla tube; anthers tetrasporangiate, dithecal, basifixed, introrsely dehiscent by longitudinal slits, the dorsal

3 longer than the ventral 2, forming a ventrally oblique tube occluded at the orifice, the ventral pair or all 5 anthers bearded at apex with dense tufts of filiform hairs, the ventral pair sometimes with a single apical bristle each, or rarely all anthers nude at apex; pollen grains tricolporate or tricolpate, prolate, ellipsoid, psilate, binucleate or trinucleate when shed. Gynoecium syncarpous, bilocular; ovary completely or partially inferior (rarely almost superior through reduction of the hypanthium); placentae axile, large; ovules numerous, small, anatropous, unitegmic, tenuinucellate; style solitary, slender, terete, with a ring of stiff white hairs below the apex; stigma bilobed, the lobes appressed and nonreceptive as the style grows through the anther tube, pushing out pollen, after which the stigmas spread and become receptive. Fruit a capsule, loculicidally dehiscent by an apical pair of triangular valves, or less often a fleshy or dry berry. Seeds small, numerous, black, brown, or golden, terete, trigonous, or lenticular (the last sometimes winged), rarely irregularly angular, cuboidal, or quadrate; testa reticulate or striate; embryo small, straight; endosperm copious, cellular, oily or rarely starchy, its formation ab initio cellular.

Chromosome numbers. $2n = 12$, 14, 16, 18, 20, 22, 24, 26, 28, 38, 42, 56, 70, 77, 84, 91, 140 (Lepper, 1979, 1980, 1982; Knox & Kowal, 1993; Lammers, 1993; Stace & James, 1996; Ruas et al., 2001; Murray et al., 2004).

Distribution. Almost cosmopolitan, native to (1) the New World, from southern Canada to Tierra del Fuego, including the Greater and Lesser Antilles, Turks and Caicos Islands, the Bahamas, Galápagos Islands, Juan Fernández Island, and the Falkland Islands; (2) northern and western Europe, from Scandinavia and northern Russia to the Iberian Peninsula, including the Faroe Islands and the British Isles; (3) Africa, in Morocco and from Senegal to Sudan and South Africa, including the Azores, Madeira, St. Helena, Madagascar, and the Mascarene Islands; (4) southern and eastern Asia, from Oman to the Russian Far East south to Indonesia and Papua New Guinea, including the Kuril Islands, Japan, the Bonin Islands, the Ryukyu Islands, Taiwan, Hainan, the Philippines, the Andaman and Nicobar Islands, and Sri Lanka; (5) Australia and New Zealand, including Norfolk, Kermadec, and Chatham islands; and (6) the central Pacific, specifically Pitcairn, Rapa, and the Hawaiian Islands. The New World and Africa are each home to over 37% of the species; 12% of the species are found in Asia, 10% in Australia and New Zealand, and 3% in the Hawaiian Islands (Lammers, 2007a). The two species native to Europe are interlopers from boreal North America (*Lobelia dortmanna*) and northwestern Africa (*L. urens* L.), while the single species native to Pitcairn and Rapa (*L. anceps* L. f.) is circumaustral, extending from southern Africa through Madagascar, Australia, Norfolk Island, New Zealand, Chatham Island, and Kermadec Island to Juan Fernández Island and Chile.

Etymology. The name honors Flemish herbalist Matthias de L'Obel (1538–1616), physician to William of Orange and James I of England, who in his *Stirpium Adversaria Nova* (1571) argued for the necessity of exacting observation in botany and medicine.

Discussion. The circumscription of *Lobelia* embraced here is that used in the recent accounts of the family in the *World Checklist and Bibliography* series (Lammers, 2007a) and the encyclopedic *Families and Genera of Vascular Plants* (Lammers, 2007c). This is nearly identical to that advocated by Schönland (1889) and Wimmer (1943, 1953, 1968); the sole difference is the inclusion of species previously assigned to *Pratia* (Moeliono, 1960; Adams, 1972; Wilbur, 1991; Murata, 1995; Lammers, 1998) and *Hypsela* (Chiapella, 1996; Lammers, 1999a). A key to distinguish the genus from the rest of the family was provided by Lammers (2007c).

This revised classification departs from its predecessors (Wimmer, 1943, 1953, 1968; Murata, 1995) in the abandonment of subgenera; the sole rank utilized here is that of section. To recognize two or three subgenera would suggest some fundamental bifurcation or trifurcation very early in the evolutionary history of the genus. The molecular phylogenies published thus far do not reveal any such event, and it does not seem likely that such a pattern will emerge with further sampling. The overall structure revealed by the most comprehensive of these (Knox et al., 2006; Antonelli, 2008) is of numerous reasonably well-defined clades with varying degrees of relatedness to one another. My opinion is that the best way to translate this sort of evolutionary structure into a traditional formal classification is to recognize multiple coordinate sections. In crafting them, I have placed primary emphasis on multiple correlations of phenotypic characters and on biogeographical coherence. To the extent that phylogenetic information is available, I have used it to inform and temper my decisions.

KEY TO THE SECTIONS OF *LOBELIA*

1a. Flowers in nodding pseudoaxillary inflorescences.
  2a. Stems erect to ascending; inflorescence corymbose, the rachis condensed; pedicels oligobracteolate; corolla 30–45 mm long; anthers nude; seeds ovoid, striate (Murata type D); plants of New Zealand ..... 3. *Lobelia* sect. *Colensoa*
  2b. Stems scrambling or sprawling; inflorescence racemose, the rachis elongate; pedicels bibracteolate below the middle; corolla 10–28 mm long; anthers with tufts of flattened hairs at apices of all five; seeds cuboidal or quadrate, reticulate (Murata type B); plants of Malesia ..... 15. *Lobelia* sect. *Plagiobotrys*
1b. Flowers in erect terminal inflorescences or solitary in the axils of the upper leaves.
  3a. Corolla lobes one fourth as long as the tube or less.
    4a. Corolla sub-bilabiate or bilabiate (rarely unilabiate), the tube straight or nearly so, the lobes free at apex; diploid plants of southern North America and northern South America ..... 11. *Lobelia* sect. *Homochilus*
    4b. Corolla unilabiate, the tube strongly arcuate, the lobes coherent at apex; hexaploid plants of central Chile ..... 12. *Lobelia* sect. *Tupa*
  3b. Corolla lobes equaling or longer than the tube.
    5a. Anthers with a single elongate bristle at the apex of each of the ventral pairs (sometimes supplemented by tufts of shorter hairs) or very rarely nude; seeds typically reticulate (Murata type B), less often striate (Murata type D); plants primarily of the Southern Hemisphere, not represented in North America.
      6a. Flowers in a corymbose or subumbellate raceme; corolla unilabiate, pink or white with transverse red or purple markings on lobes; plants of South Africa ..... 9. *Lobelia* sect. *Jasionopsis*
      6b. Flowers solitary in the axils of leaves, rarely in a loose raceme; corolla sub-bilabiate, various shades of blue, purple, pink, or white.
        7a. Plants commonly perennial; stems commonly prostrate; seed coat reticulate (Murata type B); plants of Asia, Australasia, and southern South America ..... 7. *Lobelia* sect. *Hypsela*
        7b. Plants commonly annual; stems commonly decumbent; seed coat striate (Murata type D); plants of southern Africa ..... 8. *Lobelia* sect. *Mezleriopsis*
    5b. Anthers with tufts of filiform hairs at apex of the ventral pair or all five (rarely all nude); seeds striate (Murata type D) or striate-reticulate (Murata type C), if reticulate (Murata types A and E); native to North America.
      8a. Seeds reticulate (Murata types A and E).
        9a. Stems gracile to somewhat robust, herbaceous (sometimes suffruticose at base), 5–80(–200) cm tall; bracteoles (when present) inconspicuous, typically basal or submedial on the pedicel; calyx sometimes auriculate; corolla distinctly bilabiate, various shades of blue or purple, rarely red or white, the tube straight or nearly so; seed coat reticulations roughened (Murata type A) ..... 6. *Lobelia* sect. *Lobelia*
        9b. Stems robust, commonly suffruticose or woody, (0.3–)1–4 m tall; bracteoles (when present) typically conspicuous and medial or supra-medial on the pedicel; calyx never auriculate; corolla sub-bilabiate or unilabiate, various shades of red, magenta, pink, yellow, green, or white, the tube curved to arcuate; seed coat reticulations smooth (Murata type E) ..... 10. *Lobelia* sect. *Tylomium*
      8b. Seeds striate (Murata type D) or striate-reticulate (Murata type C).
        10a. Plants annual (rarely biennial) or perennial, 0.02–0.9(–1.4) m tall; stems gracile, herbaceous (rarely suffruticose); corolla distinctly bilabiate, 3–23(–32) mm long, the lobes strongly dimorphic, the dorsal pair far shorter and narrower than the ventral three (which commonly form a trifid lip); seeds striate (Murata type D); aneuploidy common.
          11a. Pedicels (if present) typically basal; corolla tube typically fenestrate, its axis deflected ventrally from the axis of the hypanthium; staminal column included ..... 4. *Lobelia* sect. *Cryptostemon*
          11b. Pedicels (if present) typically medial or submedial; corolla tube rarely fenestrate, its axis forming a straight line with the axis of the hypanthium; staminal column exserted.
            12a. Pedicels commonly ebracteolate; only the ventral pair of anthers bearded; seeds terete or slightly compressed ..... 5. *Lobelia* sect. *Stenotium*
            12b. Pedicels bibracteolate; all five anthers bearded, or rarely nude; seeds trigonous or lenticular.
              13a. Plants commonly perennial; ventral corolla lobes all of approximately equal size and shape, forming a trifid lip; plants of Africa, Asia, and South America ..... 1. *Lobelia* sect. *Delostemon*
              13b. Plants commonly annual; central ventral corolla lobe by far the largest, forming a prominent lip, the flanking ventral lobes forming a pair of laterals; plants of Australia ..... 2. *Lobelia* sect. *Holopogon*
        10b. Plants perennial or pliestesial, (0.2–)1–9 m tall; stems robust or pachycaul, commonly suffruticose or woody; corolla unilabiate or sub-bilabiate (rarely bilabiate), (12–)18–103 mm long, the lobes monomorphic or scarcely dimorphic, all similar in size and shape; testa striate-reticulate (Murata type C); aneuploidy unknown.

14a. Leaves petiolate (sessile in one Chinese species); flowers solitary in the axils of the upper leaves (rarely supplemented by a few-flowered terminal raceme); corolla 12–26 mm long.
15a. Corolla white, 12–15 mm long, the tube slightly curved; fruit a capsule; plants of St. Helena ..... 13. *Lobelia* sect. *Trimeris*
15b. Corolla greenish, red-purple, or dark violet (lip often contrastingly striped or spotted), (12–)18–26 mm long, the tube straight; fruit a berry; plants of Asia ..... 14. *Lobelia* sect. *Speirema*
14b. Leaves sessile (petiolate in two rare species); flowers in a many-flowered terminal raceme or panicle; corolla (12–)25–103 mm long.
16a. Pedicels ebracteolate; corolla 45–103 mm long; all five anthers bearded; plants of Hawaii ..... 18. *Lobelia* sect. *Galeatella*
16b. Pedicels commonly bibracteolate; corolla (12–)25–50 mm long; only the ventral anthers bearded (rarely all nude).
17a. Corolla tube curved or arcuate, the lobes spreading; seeds lenticular and commonly winged; plants of Asia, Africa, and South America ..... 16. *Lobelia* sect. *Rhynchopetalum*
17b. Corolla tube straight or nearly so, the lobes recoiled; seeds terete; plants of Hawaii ..... 17. *Lobelia* sect. *Revolutella*

1. Lobelia sect. **Delostemon** (E. Wimm.) J. Murata, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15: 356. 1995. *Lobelia* subsect. *Delostemon* E. Wimm., Ann. Naturhist. Mus. Wien 56: 359. 1948. TYPE [designated by J. Murata, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15: 356. 1995]: *Lobelia alsinoides* Lam.

Lobelia grex *Gratioloides* E. Wimm., Ann. Naturhist. Mus. Wien 56: 360. 1948. TYPE [here designated]: *Lobelia alsinoides* Lam.

Lobelia grex *Genistoides* E. Wimm., Ann. Naturhist. Mus. Wien 56: 362. 1948. TYPE [sub Art. 22.6]: *Lobelia genistoides* (C. Presl) A. DC. [= *Lobelia patula* L. f.].

Plants perennial (hemicryptophytes, geophytes, or chamaephytes) or annual, 6–60 cm tall; one species (*Lobelia aquatica* Cham.) hydrophytic. Stems gracile, herbaceous or sometimes suffruticose, prostrate, decumbent, ascending, or erect, simple to branched, sometimes stoloniferous, caespitose, or radicant. Leaves sessile or petiolate. Flowers solitary in the axils of the upper leaves or these much reduced, creating a terminal sometimes secund raceme; pedicels bibracteolate at or below the middle. Corolla bilabiate, typically some shade of blue or purple, less often pink or white, 5–20(–32) mm; tube straight, cleft almost to its base on the dorsal side (laterally fenestrate in *Lobelia stenocarpa* E. Wimm.); lobes strongly dimorphic, spreading, almost as long as the tube to longer than the tube, often with a palate or a pair of yellow or white gibbosities on the ventral lip at the mouth of the tube. Staminal column exserted; anthers bearded with tufts of filiform hairs at apex on all 5 (those on the ventral pair sometimes longer). Fruit a capsule. Seeds ovoid to oblong, trigonous or lenticular; testa striate (Murata type D).

Chromosome numbers. $2n = 12, 14, 28$ (Lammers, 1993).

Distribution. Forty-four species in four general regions: (1) Southern Africa: Angola to Mozambique and south, with the greatest concentration of species in the Cape Provinces. Included species: *Lobelia ardisiandroides* Schltr., *L. barkerae* E. Wimm., *L. caerulea* Sims, *L. capillifolia* (C. Presl) A. DC., *L. chamaedryifolia* (C. Presl) A. DC., *L. chamaepitys* Lam., *L. cochlearifolia* Diels, *L. comptonii* E. Wimm., *L. corniculata* Thulin, *L. coronopifolia* L., *L. dasyphylla* E. Wimm., *L. decurrentifolia* (Kuntze) K. Schum., *L. dichroma* Schltr., *L. eurypoda* E. Wimm., *L. linearis* Thunb., *L. malowensis* E. Wimm., *L. neglecta* Schult., *L. patula* L. f., *L. pinifolia* L., *L. preslii* A. DC., *L. pteropoda* (C. Presl) A. DC., *L. setacea* Thunb., *L. thermalis* Thunb., *L. tomentosa* L. f., *L. vanreenensis* (Kuntze) K. Schum. (2) Tropical Africa: Senegal to Ethiopia, Mozambique, and Angola, with *L. goetzei* extending south to Transvaal and *L. stenocarpa* endemic to Madagascar. Included species: *L. baumannii* Engl., *L. blantyrensis* E. Wimm., *L. cobaltica* S. Moore, *L. djurensis* Engl. & Diels, *L. goetzei* Diels, *L. hartlaubii* Buchenau, *L. holstii* Engl., *L. humpatensis* E. Wimm., *L. ovina* E. Wimm., *L. stenocarpa* E. Wimm. (3) Southern and eastern Asia: India and Sri Lanka to Japan, the Ryukyu Islands, Taiwan, the Andaman and Nicobar Islands, the Philippines, and New Guinea. Included species: *L. alsinoides* Lam., *L. chevalieri* Danguy, *L. griffithii* Hook. f. & Thomson, *L. macraeana* E. Wimm., *L. microcarpa* C. B. Clarke, *L. terminalis* C. B. Clarke, *L. zeylanica* L. (4) South America: Colombia to French Guiana and northeastern Argentina; the first species also occurs on Hispaniola. Included species: *L. aquatica* Cham., *L. nummularioides* Cham.

Discussion. The circumscription used here is identical to that of Murata (1995); in Wimmer's (1953, 1968) treatment, it would be equivalent to his *Lobelia* subsect. *Delostemon*, minus *Lobelia* grex

Impares (see below). In recent molecular studies (Knox et al., 2006; Antonelli, 2008), the species of this section plus the next two fell into two clades at the base of the phylogeny. The former also indicated that, if one were to take a strictly cladistic approach to classification, *Grammatotheca* and *Monopsis* might be assigned to this section. If so, the correct name would be a new combination based on *Rapuntium* sect. *Xanthomeria*. If *Monopsis* were retained as a distinct genus, the correct name would be a new combination based on *Rapuntium* sect. *Grammatotheca* (C. Presl) Kuntze.

2. Lobelia sect. **Holopogon** Benth., Fl. Austral. 4: 122. 1869. *Rapuntium* sect. *Holopogon* (Benth.) Kuntze, Lex. Gen. Phan. 478. 1903. TYPE [designated by J. Murata, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15: 357. 1995]: *Lobelia gibbosa* Labill.

Lobelia grex *Impares* E. Wimm., Ann. Naturhist. Mus. Wien 56: 359. 1948. TYPE [here designated]: *Lobelia heterophylla* Labill.

Plants annual or rarely perennial (hemicryptophytes), (2–)10–40(–60) cm tall. Stems gracile, herbaceous, decumbent, ascending, or erect, simple to branched. Leaves sessile or petiolate. Flowers solitary in the axils of the upper leaves or these reduced in size, creating a terminal sometimes secund raceme (rarely a panicle); pedicels bibracteolate near middle. Hypanthium sometimes dorsally distended. Corolla bilabiate, various shades of blue or purple, sometimes marked with yellow, 8–30 mm; tube straight or somewhat curved, cleft almost to its base on the dorsal side, rarely only partway; lobes strongly dimorphic, almost as long as the tube to longer than the tube, spreading, the odd lobe larger than the lateral pair or dorsal pair. Staminal column exserted; anthers bearded with tufts of filiform hairs at apex of all 5 (very rarely all nude). Fruit a capsule. Seeds ovoid or ellipsoid, trigonous or lenticular; testa striate (Murata type D).

Chromosome numbers. $2n = 16, 18, 20, 22$ (Lammers, 1993; Stace & James, 1996).

Distribution. Endemic to Australia; 14 species. Included species: *Lobelia andrewsii* Lammers, *L. dentata* Cav., *L. gibbosa* Labill., *L. gouldii* W. Fitzg., *L. heterophylla* Labill., *L. leichhardii* E. Wimm., *L. psilostoma* E. Wimm., *L. rarifolia* E. Wimm., *L. rhombifolia* de Vriese, *L. rhytidosperma* Benth., *L. simplicicaulis* R. Br., *L. tenuior* R. Br., *L. trigonocaulis* F. Muell., *L. winifrediae* Diels.

Discussion. The circumscription used here is essentially the same as that adopted by Bentham (1876), Schönland (1889), and Post and Kuntze (1903); it is supported by a recent phylogenetic analysis (Knox et al., 2006). Wimmer's (1953, 1968) circumscription of *Lobelia* sect. *Holopogon*, however, was much broader, encompassing diverse extra-Australian species; the section as treated here is equivalent to his *Lobelia* grex *Impares* only. Murata (1995) did not recognize a taxon equivalent to this section, but merely included its species within his *Lobelia* sect. *Pratia*.

Molecular phylogenetic studies (E. Knox, pers. comm.) indicate that the type of *Isotoma* (R. Br.) Lindl., *Lobelia hypocrateriformis* R. Br., logically might be referred to this section (though the remainder of that genus would be referable to *Lobelia* sect. *Hypsela* (C. Presl) Lammers [Heenan et al., 2008; Knox et al., 2008a]). If that species were to be transferred here, the name of the section would not be affected.

3. Lobelia sect. **Colensoa** (Hook. f.) J. Murata, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15: 358. 1995. *Colensoa* Hook. f., Bot. Antarct. Voy. II. (Fl. Nov.-Zel.) 1: 156. 1852. *Pratia* sect. *Colensoa* (Hook. f.) Baill., Hist. Pl. 8: 366. 1885. TYPE [sub Art. 37.3]: *Colensoa physaloides* (A. Cunn.) Hook. f. [≡ *Lobelia physaloides* A. Cunn.].

Plants perennial (chamaephytes), 0.3–1 m tall. Stems robust, suffruticose toward base, herbaceous toward apex, sparingly branched, erect to ascending. Leaves long petiolate, prominently serrate. Inflorescence a nodding 5- to 20-flowered pedunculate pseudoaxillary corymbose raceme; pedicels oligobracteolate. Corolla bilabiate, purple or blue, sometimes very pale, 30–45 mm; tube suberect, dorsally cleft to base; lobes monomorphic, almost as long as the tube to longer than the tube, spreading, the dorsal pair nearly distinct, the ventral 3 forming a trifid lip. Staminal column exserted; anthers nude at apex. Fruit a dark blue, globose, fleshy or leathery berry. Seeds ovoid, terete; testa striate (Murata type D).

Chromosome number. $2n = 26$ (Lammers, 1993).

Distribution. Endemic to New Zealand's North Island; monotypic. Included species: *Lobelia physaloides* A. Cunn.

Discussion. Wimmer (1943, 1953, 1968) assigned this section to *Pratia* and included not only *Lobelia physaloides* but also species referable to

Lobelia sect. *Speirema* (Hook. f. & Thomson) Lammers, *Lobelia* sect. *Plagiobotrys* Lammers, and *Lobelia* sect. *Tylomium*. Murata (1995) transferred the section to *Lobelia* subg. *Tupa*, but likewise circumscribed it broadly, encompassing species now assigned to *Lobelia* sect. *Speirema*, *Lobelia* sect. *Plagiobotrys*, and *Lobelia* sect. *Rhynchopetalum*.

The present classification differs from these in restricting the section to its type. This species' subcorymbose pseudoaxillary inflorescence and oligobracteolate pedicels are unique within the genus. Furthermore, in recent molecular phylogenies (Knox et al., 2006; Antonelli, 2008), *Lobelia physaloides* was not related to species of *Lobelia* sect. *Tylomium* or *Lobelia* sect. *Rhynchopetalum* (exemplars of *Lobelia* sect. *Speirema* and *Lobelia* sect. *Plagiobotrys* have yet to be sequenced); instead, it belonged to a clade comprising species of *Lobelia* sect. *Delostemon* and *Lobelia* sect. *Holopogon*. Because *L. physaloides* differs from these two sections in both vegetative and floral morphology, I sequester it in its own monotypic section.

Practical references. Excellent illustrations of this unusual species accompany papers by the Hookers, father (1843) and son (1886).

4. Lobelia sect. **Cryptostemon** (E. Wimm.) J. Murata, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15: 356. 1995. *Lobelia* subsect. *Cryptostemon* E. Wimm., Ann. Naturhist. Mus. Wien 56: 358. 1948. TYPE [designated by J. Murata, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15: 356. 1995]: *Lobelia fenestralis* Cav.

Plants perennial (hemicryptophytes or geophytes) or rarely annual, (4–)20–90(–140) cm tall. Roots often tuberous. Stems gracile or somewhat robust, herbaceous, erect (rarely decumbent), simple or sometimes sparingly branched, rarely rhizomatous. Leaves sessile or subsessile, often clasping or auriculate, only the rarely present radical leaves petiolate. Flowers in a terminal, often pedunculate spiciform and often secund (rarely subumbellate) raceme; pedicels ebracteolate or bibracteolate at base (rarely middle). Corolla bilabiate, various shades of blue or purple (rarely white), 7–17(–26) mm; tube straight but its axis deflexed ventrally relative to the axis of the hypanthium, typically cleft on the dorsal side almost to its base (rarely only fenestrate at base) and laterally fenestrate (rarely entire); lobes strongly dimorphic, almost as long as the tube to longer than the tube, spreading. Staminal column included; anthers bearded with tufts of filiform hairs at apex of all 5. Fruit a capsule. Seeds ellipsoid, terete; testa striate (Murata type D).

Chromosome number. Unknown (Lammers, 1993).

Distribution. Endemic to the New World, with nine species from the southwestern United States to Panama, and *Lobelia holotricha* E. Wimm. endemic to Peru. Included species: *L. fenestralis* Cav., *L. hartwegii* A. DC. ex Benth., *L. holotricha* E. Wimm., *L. irasuensis* Planch. & Oerst., *L. jaliscensis* McVaugh, *L. macdonaldii* B. L. Turner, *L. poetica* E. Wimm., *L. sinaloae* Sprague, *L. umbellifera* McVaugh.

Discussion. The treatment here is identical to that of Murata (1995); Wimmer's (1953, 1968) circumscription of the taxon was the same, but it was ranked and positioned as a subsection of *Lobelia* sect. *Holopogon*. Though the species of *Lobelia* sect. *Cryptostemon* do possess five bearded anthers like *Lobelia* sect. *Holopogon*, they do not produce the distinctive trigonous or lenticular seeds of that section. Furthermore, a close relationship between an Australian and a fundamentally North American group seems unlikely.

The molecular phylogeny of Koopman and Ayers (2005) suggested that the section may be biphyletic: *Lobelia irasuensis* belonged to a clade composed largely of North American species of *Lobelia* sect. *Stenotium* (C. Presl) Lammers, while *L. fenestralis* was sister to the type of *Lobelia* sect. *Homochilus*. In Antonelli's (2008) analysis, the sole exemplar of *Lobelia* sect. *Cryptostemon* was part of a clade that included all sampled species of *Lobelia* sect. *Homochilus* and *Lobelia* sect. *Tylomium*, plus North American representatives of *Lobelia* sect. *Stenotium*. Further sampling is needed to resolve these phylogenetic relationships, but on the basis of overall morphology, including that of the seeds, a relationship to *Lobelia* sect. *Stenotium* seems the more likely.

5. Lobelia sect. **Stenotium** (C. Presl) Lammers, Fl. China 19: 556. 2011. *Rapuntium* sect. *Stenotium* C. Presl, Prodr. Monogr. Lobel. 11. 1836. *Lobelia* [unranked] *Stenotium* (C. Presl) Benth., Enum. Pl. [Endlicher] 74. 1837. TYPE [here designated]: *Rapuntium erinus* (L.) Mill. [≡ *Lobelia erinus* L.].

Enchysia C. Presl, Prodr. Monogr. Lobel. 40. 1836. *Laurentia* [unranked] *Enchysia* (C. Presl) Endl., Gen. Pl. 512. 1838. *Lobelia* [unranked] *Enchysia* (C. Presl) Heynh., Nomencl. Bot. Hort. 1: 470. 1840. *Laurentia* subg. *Enchysia* (C. Presl) Peterm., Pflan-

zenreich 444. 1845. TYPE [designated by Pfeiffer, Nomencl. Bot. 1: 1199. 1874]: *Lobelia erinoides* L. [= *Lobelia erinus* L.].

Lobelia [unranked] *Xalapenses* Small, Man. S.E. Fl. 1291. 1933. TYPE [sub Art. 22.6]: *Lobelia xalapensis* Kunth.

Lobelia grex *Subspicatae* E. Wimm., Ann. Naturhist. Mus. Wien 56: 341. 1948. TYPE [here designated]: *Lobelia gruina* Cav.

Lobelia grex *Rosulatae* E. Wimm., Ann. Naturhist. Mus. Wien 56: 342. 1948. TYPE [here designated]: *Lobelia lepida* E. Wimm.

Lobelia grex *Pterocaulinae* E. Wimm., Ann. Naturhist. Mus. Wien 56: 343. 1948. TYPE [here designated]: *Lobelia anceps* L. f.

Lobelia grex *Eriniformes* E. Wimm., Ann. Naturhist. Mus. Wien 56: 346. 1948. TYPE [sub Art. 22.6]: *Lobelia erinus* L.

Lobelia [unranked] *Pusillae* E. Wimm., Pflanzenr. IV, 276b: 496. 1953. TYPE [here designated]: *Lobelia erlangeriana* Engl.

Lobelia [unranked] *Subgrandiflores* E. Wimm., Pflanzenr. IV, 276b: 500. 1953. TYPE [here designated]: *Lobelia sublibera* S. Watson.

Lobelia [unranked] *Latifoliae* E. Wimm., Pflanzenr. IV, 276b: 502. 1953. TYPE [here designated]: *Lobelia berlandieri* A. DC.

Lobelia [unranked] *Angustifoliae* E. Wimm., Pflanzenr. IV, 276b: 533. 1953. TYPE [here designated]: *Lobelia linarioides* (C. Presl) A. DC.

Lobelia [unranked] *Dissectifoliae* E. Wimm., Pflanzenr. IV, 276b: 552. 1953. TYPE [sub Art. 22.6]: *Lobelia dissecta* M. B. Moss.

Heterotoma sect. *Microcentron* E. Wimm., Pflanzenr. IV, 276b: 716. 1953. TYPE [here designated]: *Heterotoma cordifolia* (Hook. & Arn.) McVaugh [≡ *Lobelia cordifolia* Hook. & Arn.].

Lobelia sect. *Heyneana* J. Murata, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15: 355. 1995. TYPE [designated by the author]: *Lobelia heyneana* Schult.

Calcaratolobelia Wilbur, Sida 17: 561. 1997. TYPE [designated by the author]: *Calcaratolobelia cordifolia* (Hook. & Arn.) Wilbur [≡ *Lobelia cordifolia* Hook. & Arn.].

Plants annual or perennial (commonly hemicryptophytes, less often geophytes or chamaephytes), 2–50(–90) cm tall. Stems gracile, herbaceous or suffruticose, prostrate, decumbent, ascending, or erect, sometimes rhizomatous or stoloniferous, terete to sharply 3- to 4-angled or -winged; latex white (rarely orange). Leaves sessile or petiolate. Flowers solitary in the axils of the upper leaves or these reduced in size, creating a terminal, sometimes secund raceme (rarely spiciform or corymbose); pedicels ebracteolate or bibracteolate at or below (rarely above) the middle. Corolla bilabiate, 3–20(–24) mm, various shades of blue, purple, pink, or white; tube straight or somewhat curved, typically cleft almost to its base (rarely only to the middle) on the dorsal side, rarely fenestrate, sometimes the ventral side prolonged into a distinct short or long slender nectar spur that distends the hypanthium; lobes strongly dimorphic, almost as long as the tube to longer than the tube, spreading, sometimes with a pair of gibbosities on the ventral lip at the mouth of the tube. Staminal column exserted; anthers bearded with tufts of filiform hairs (rarely also with a single apical bristle each) at apex of the ventral pair. Ovary sometimes almost superior through reduction of the hypanthium. Fruit a capsule or rarely baccate. Seeds ovoid to oblong, terete or somewhat compressed; testa striate (Murata type D).

Chromosome numbers. $2n = 12$, 14, 24, 26, 28, 38, 42 (Lammers, 1993; Stace & James, 1996).

Distribution. One hundred forty-four species in eight major regions: (1) Continental North America: southern United States to Panama, with *Lobelia nana* Kunth and *L. xalapensis* extending south to Argentina and *L. fastigiata* Kunth to eastern Brazil (chromosome numbers: $2n = 14$, 28). Included species: *L. anatina* E. Wimm., *L. aurita* (Brandegee) T. J. Ayers, *L. berlandieri* A. DC., *L. caeciliae* E. Wimm., *L. circaeoides* (C. Presl) A. DC., *L. cordifolia* Hook. & Arn., *L. diastateoides* McVaugh, *L. diazlunae* Rzed. & Calderón, *L. dielsiana* E. Wimm., *L. divaricata* Hook. & Arn., *L. ehrenbergii* Vatke, *L. endlichii* (E. Wimm.) T. J. Ayers, *L. fastigiata* Kunth, *L. flexicaulis* Rzed. & Calderón, *L. flexuosa* (C. Presl) A. DC., *L. gladiaria* McVaugh, *L. glaucescens* E. Wimm., *L. goldmanii* (Fernald) T. J. Ayers, *L. gruina* Cav., *L. gypsophila* T. J. Ayers, *L. henricksonii* M. C. Johnst., *L. hintoniorum* B. L. Turner, *L. homophylla* E. Wimm., *L. hypnodes* E. Wimm. ex McVaugh, *L. illota* McVaugh, *L. knoblochii* T. J. Ayers, *L. lithophila* Senterre & Cast.-Campos, *L. longicaulis* Brandegee, *L. macrocentron* (Benth.) T. J. Ayers, *L. margarita* E. Wimm., *L. mcvaughii* T. J. Ayers, *L. mexicana* E. Wimm., *L. nana* Kunth, *L. obconica* E. Wimm., *L. occidentalis* McVaugh & Huft, *L. orientalis* Rzed. & Calderón, *L. porphyrea* Rzed. & Calderón, *L. pringlei* S. Watson, *L. pulchella* Vatke, *L. purpusii* Brandegee, *L. sartorii* Vatke, *L. scrobiculata* E. Wimm., *L. standleyi* McVaugh, *L. stenodonta* (Fernald) McVaugh, *L. stolonifera* Donn. Sm., *L. sublibera* S. Watson, *L. subnuda* Benth., *L. tarsophora* Seaton ex Greenm., *L. villaregalis* T. J. Ayers, *L. volcanica* T. J. Ayers, *L. xalapensis* Kunth, *L. yucatana* E. Wimm. (2) Caribbean (chromosome numbers: $2n = 14$, 28). Included species: *Lobelia cliffortiana* L. (Antilles), *L. lucayana* Britton & Millsp. (Bahamas, Turks and Caicos Islands). (3) South America: Venezuela to Peru and northern Argentina. Included species: *L. camporum* Pohl, *L. collina* Kunth, *L. luruniensis* E. Wimm., *L. modesta* Wedd., *L. paranaensis* R. Braga,

L. subpubera Wedd., *L. tenera* Kunth. (4) Northwestern Africa (Morocco), western Europe (Iberian Peninsula to France and southern Britain), and Macaronesia (Azores, Madeira) (chromosome number: $2n = 14$). Included species: *L. urens* L. (5) Tropical Africa: Senegal to Somalia and Mozambique, with *L. erinus* L. and *L. trullifolia* Hemsl. extending to southern Africa (chromosome numbers: $2n = 12, 14, 26, 28, 38, 42$). Included species: *L. acutidens* Hook. f., *L. adnexa* E. Wimm., *L. cheranganiensis* Thulin, *L. chireensis* A. Rich., *L. cymbalarioides* Engl., *L. dissecta* M. B. Moss, *L. duriprati* T. C. E. Fr., *L. erinus* L., *L. erlangeriana* Engl., *L. exilis* Hochst. ex A. Rich., *L. fervens* Thunb., *L. flaccida* (C. Presl) A. DC., *L. gilgii* Engl., *L. gilletii* De Wild., *L. gracillima* Welw. ex Hiern, *L. graniticola* E. Wimm., *L. henodon* E. Wimm., *L. inconspicua* A. Rich., *L. intercedens* (E. Wimm.) Thulin, *L. kalobaensis* E. Wimm. ex Thulin, *L. kirkii* R. E. Fr., *L. kundelungensis* Thulin, *L. lasiocalycina* E. Wimm., *L. lepida* E. Wimm., *L. lindblomii* Mildbr., *L. lisowskii* Thulin, *L. livingstoniana* R. E. Fr., *L. lobata* E. Wimm., *L. minutula* Engl., *L. molleri* Henriq., *L. neumannii* T. C. E. Fr., *L. paludigena* Thulin, *L. quarreana* E. Wimm., *L. rivalis* E. Wimm., *L. rubescens* De Wild., *L. sapinii* De Wild., *L. scebelii* Chiov., *L. schimperi* Hochst. ex A. Rich., *L. tripartita* Thulin, *L. trullifolia* Hemsl., *L. uliginosa* E. Wimm., *L. welwitschii* Engl. & Diels. (6) Southern Africa: Namibia and the Cape Provinces to Natal and Swaziland, with *L. anceps* L. f. extending east to Mozambique, Madagascar, Australia, Norfolk Island, New Zealand, Kermadec Island, Chatham Island, Rapa, Pitcairn Island, Juan Fernández Island, and Chile (chromosome numbers: $2n = 14, 42$). Included species: *Lobelia anceps* L. f., *L. aquaemontis* E. Wimm., *L. boivinii* Sond., *L. comosa* L., *L. cuneifolia* Link & Otto, *L. cyphioides* Harv., *L. dregeana* (C. Presl) A. DC., *L. filipes* E. Wimm., *L. galpinii* Schltr., *L. hereroensis* Schinz, *L. hypsibata* E. Wimm., *L. laurentioides* Schltr., *L. laxa* MacOwan, *L. linarioides* (C. Presl) A. DC., *L. muscoides* Cham., *L. oreas* E. Wimm., *L. parvisepala* E. Wimm., *L. pentheri* E. Wimm., *L. pubescens* Aiton, *L. reinekeana* E. Wimm., *L. stenosiphon* (Adamson) E. Wimm., *L. sutherlandii* E. Wimm., *L. valida* L. Bolus, *L. wilmsiana* Diels. (7) Madagascar and the Mascarenes. Included species: *L. agrestis* E. Wimm., *L. cyanea* E. Wimm., *L. filiformis* Lam., *L. hirtipes* E. Wimm., *L. horombensis* E. Wimm., *L. lingulata* E. Wimm., *L. parva* Badré & Cadet, *L. perrieri* E. Wimm., *L. serpens* Lam., *L. solaris* E. Wimm., *L. spathopetala* Diels, *L. telephioides* (C. Presl) A. DC., *L. vagans* Balf. f. (8) Southern and eastern Asia: Oman to China, Taiwan, the Philippines, and New Guinea, with *L. heyneana* Schult. extending into tropical Africa (Ethiopia to Zaire and Zambia) (chromosome number: $2n = 24$). Included species: *Lobelia hainanensis* E. Wimm., *L. heyneana* Schult., *L. luzoniensis* (Pers.) Merr.

Discussion. This section is nearly identical to Murata's (1995) *Lobelia* sect. *Heyneana*; the name change is dictated by the rules of priority. It is likewise similar to Wimmer's (1953, 1968) *Lobelia* subsect. *Leiospermae*, with two exceptions: (1) the exclusion of *Lobelia* grex *Dioicae* (here assigned to *Lobelia* sect. *Hypsela*), and (2) the inclusion of all species of *Heterotoma* Zucc. save its type (cf. Ayers, 1990; Wilbur, 1997).

In Koopman and Ayers' (2005) molecular phylogeny, the sampled species (all North American) fell into a single clade. The preliminary results of Knox et al. (2006) and Antonelli (2008), however, suggest that the section may be polyphyletic along geographic lines. Far more sampling will be required to resolve the issue. Assignment of the genus *Wimmerella* Serra, M. B. Crespo & Lammers to this section (cf. Knox et al., 2006) would not affect its name.

6. Lobelia L. sect. **Lobelia**.

Rapuntium Mill., Gard. Dict. Abr., ed. 4. 1754. *Lobelia* sect. *Rapuntium* (Mill.) A. DC., Prodr. (DC.) 7: 357. 1839. TYPE [designated by Lammers, World Checkl. Bibliogr. Campanulaceae: 509. 2007]: *Rapuntium cardinale* (L.) Mill. [≡ *Lobelia cardinalis* L.]. [Although *Lobelia* sect. *Rapuntium* must be replaced by this autonym (Art. 22.1), the former nevertheless was validly published because it did not include all elements eligible as the type of *Lobelia* at that time (Art. 22.2).]

Dortmanna O. O. Rudbeck ex Hill, Brit. Herb. 126. 1756. *Lobelia* [unranked] *Dortmanna* (O. O. Rudbeck ex Hill) Endl., Gen. Pl. 512. 1838. *Rapuntium* sect. *Dortmanna* (O. O. Rudbeck ex Hill) Kuntze, Lex. Gen. Phan. 477. 1903, as "*Dortmannia*." TYPE [sub Art. 37.3]: *Lobelia dortmanna* L.

Rapuntium sect. *Sphaerangium* C. Presl, Prodr. Monogr. Lobel. 19. 1836. *Lobelia* [unranked] *Sphaerangium* (C. Presl) Endl., Gen. Pl. 511. 1838. TYPE [here designated]: *Rapuntium siphiliticum* (L.) Mill. [≡ *Lobelia siphilitica* L.].

Lobelia sect. *Eulobelia* Benth., Gen. Pl. [Bentham & Hooker f.] 2: 552. 1876, nom. invalid. sub Art. 21.3.

Rapuntium sect. *Cardinalis* Kuntze, Lex. Gen. Phan. 477. 1903. TYPE [sub Art. 22.6]: *Lobelia cardinalis* L. [This name was validly published because the type of the genus had not yet been designated and the taxon represented did not include all species eligible as type of the genus (Art. 22.2).]

Petromarula Belli ex Nieuwl. & Lunell, Amer. Midl. Naturalist 5: 13. 1917, nom. illeg. sub Art. 53.1, non *Petromarula* Vent. ex R. Hedw., Gen. Pl. 139. 1806. TYPE [designated by Lammers, World Checkl. Bibliogr. Campanulaceae: 509. 2007]: *Petromarula hirtella* (A. Gray) Nieuwl. & Lunell [= *Lobelia spicata* Lam.].

Lobelia [unranked] *Appendiculatae* Small, Man. S.E. Fl. [Small] 1291. 1933. TYPE [sub Art. 22.6]: *Lobelia appendiculata* A. DC.

Lobelia [unranked] *Spicatae* Small, Man. S.E. Fl. [Small] 1291. 1933. TYPE [sub Art. 22.6]: *Lobelia spicata* Lam.

Lobelia [unranked] *Nuttallianae* Small, Man. S.E. Fl. [Small] 1291. 1933. TYPE [sub Art. 22.6]: *Lobelia nuttallii* Schult.

Lobelia [unranked] *Paludosae* Small, Man. S.E. Fl. [Small] 1291. 1933. TYPE [sub Art. 22.6]: *Lobelia paludosa* Nutt.

Lobelia [unranked] *Siphiliticae* Small, Man. S.E. Fl. [Small] 1291. 1933. TYPE [sub Art. 22.6]: *Lobelia siphilitica* L.

Lobelia subg. *Lagotis* E. Wimm., Ann. Naturhist. Mus. Wien 56: 338. 1948, nom. invalid. sub Art. 22.2.

Lobelia subsect. *Trachyspermae* E. Wimm., Ann. Naturhist. Mus. Wien 56: 338. 1948, nom. invalid. sub Art. 22.2.

Lobelia grex *Cardinales* E. Wimm., Ann. Naturhist. Mus. Wien 56: 338. 1948, nom. invalid. sub Art. 22.2.

Lobelia grex *Coelestes* E. Wimm., Ann. Naturhist. Mus. Wien 56: 340. 1948. TYPE [here designated]: *Lobelia siphilitica* L.

Lobelia subgrex *Kalmia* E. Wimm., Ann. Naturhist. Mus. Wien 56: 340. 1948. TYPE [sub Art. 37.3]: *Lobelia siphilitica* L. [Although one might think that *Lobelia kalmii* would be the type of this name under Article 22.6, it was not mentioned in the protologue.]

Lobelia subgrex *Dortmannia* E. Wimm., Ann. Naturhist. Mus. Wien 56: 340. 1948. TYPE [sub Art. 37.3]: *Lobelia dortmanna* L.

Plants perennial (hemicryptophytes), less often annual or biennial, 5–80(–200) cm tall, rarely hydrophytic, a few species sometimes gynodioecious. Stems gracile (rarely somewhat robust), herbaceous (sometimes suffruticose at base), decumbent, ascending, or erect, simple to much branched, sometimes basally rosulate. Leaves sessile or petiolate. Flowers in a terminal raceme (sometimes secund); pedicels bibracteolate at base (rarely near middle, or ebracteolate). Calyx sometimes with a reflexed auriculate appendage in each sinus. Corolla bilabiate, various shades of blue or purple, often with a white eye, or rarely red or white (red in *Lobelia cardinalis*), 5–20(–46) mm; tube straight, cleft almost to its base on the dorsal side, sometimes laterally fenestrate; lobes strongly dimorphic, almost as long as the tube to longer than the tube, spreading, sometimes with a pair of green or white gibbosities on the ventral lip at the mouth of the tube. Anthers bearded with tufts of filiform hairs at the apex of the ventral pair. Fruit a capsule. Seeds ovoid, ellipsoid, or oblong, terete or irregularly angular; testa roughened reticulate (Murata type A).

Chromosome numbers. $2n = 14, 28, 42$ (Lammers, 1993).

Distribution. Nearly endemic to eastern and central North America, with *Lobelia cardinalis* extending west to California and south through Mexico and Central America to Colombia, and *L. dortmanna* extending eastward into northern Europe; 22 species. Included species: *Lobelia amoena* Michx., *L. appendiculata* A. DC., *L. boykinii* Torr. & A. Gray ex A. DC., *L. brevifolia* Nutt. ex A. DC., *L. canbyi* A. Gray, *L. cardinalis* L., *L. dortmanna* L., *L. elongata* Small, *L. feayana* A. Gray, *L. flaccidifolia* Small, *L. floridana* Chapm., *L. gattingeri* A. Gray, *L. georgiana* McVaugh, *L. glandulosa* Walter, *L. inflata* L., *L. kalmii* L., *L. nuttallii* Schult., *L. paludosa* Nutt., *L. puberula* Michx., *L. reverchonii* B. L. Turner, *L. siphilitica* L., *L. spicata* Lam.

Discussion. The circumscription used here is identical to that of Murata (1995). Wimmer's (1953, 1968) circumscription, however, was much broader, encompassing diverse Old World species as well; the section as treated here is equivalent to his *Lobelia* subsect. *Trachyspermae*. The molecular phylogeny of Antonelli (2008) supports the present circumscription, but suggests that Antillean *L. rotundifolia* Juss. ex A. DC. may belong here rather than in *Lobelia* sect. *Tylomium* (cf. McVaugh, 1943).

Practical references. A key and detailed descriptions for these species were provided by McVaugh (1943).

7. Lobelia sect. **Hypsela** (C. Presl) Lammers, Fl. China 19: 555. 2011. *Hypsela* C. Presl, Prodr. Monogr. Lobel. 45. 1836. *Lysipomia* sect. *Hypsela* (C. Presl) A. DC., Prodr. (DC.) 7: 350. 1839. *Pratia* sect. *Hypsela* (C. Presl) Baill., Hist. Pl. 8: 366. 1885. TYPE [sub Art. 37.3]: *Hypsela reniformis* (Kunth) C. Presl [= *Lobelia oligophylla* (Wedd.) Lammers].

Pratia Gaudich., Ann. Sci. Nat. (Paris) 5: 103. 1825. *Pratia* [unranked] *Eupratia* Endl., Gen. Pl. 512. 1838, nom. invalid. sub Art. 21.3. *Lobelia* [unranked] *Pratia* (Gaudich.) Heynh., Nomencl. Bot. Hort. 1: 473. 1840. *Lobelia* sect. *Pratia* (Gaudich.) J. Murata, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15: 356. 1995, nom. invalid. sub Art. 33.4. TYPE [sub Art. 37.3]: *Pratia repens* Gaudich. [≡ *Lobelia pratiana* Gaudich. ex Lammers].

Holostigma G. Don, Gen. Hist. 3: 716. 1834. *Monopsis* [unranked] *Holostigma* (G. Don) Endl., Gen. Pl. 511. 1838. *Holostigmateia* Rchb., Deut. Bot. Herb.-Buch 57. 1841, nom. illeg. sub Art. 52.1. TYPE [sub Art. 37.3]: *Holostigma dioicum* (R. Br.) G. Don [≡ *Lobelia dioica* R. Br.].

Pratia [unranked] *Bernonia* Endl., Gen. Pl. 512. 1838. *Bernonia* (Endl.) Meisn., Pl. Vasc. Gen. [Meisner] 148. Aug 1839. *Piddingtonia* A. DC., Prodr. (DC.) 7:

341. Dec. 1839, nom. illeg. sub Art. 52.1. *Lobelia* [unranked] *Piddingtonia* Heynh., Nomencl. Bot. Hort. 1: 473. 1840, nom. illeg. sub Art. 52.1. TYPE [sub Art. 37.3]: *Lobelia begoniifolia* Wall. [= *Lobelia nummularia* Lam.].

Isolobus A. DC., Prodr. (DC.) 7: 352. 1839. *Lobelia* [unranked] *Isolobus* (A. DC.) Heynh., Nomencl. Bot. Hort. 1: 471. 1840. *Monopsis* [unranked] *Isolobus* (A. DC.) Endl., Gen. Pl. 1391. 1841. *Lobelia* sect. *Isolobus* (A. DC.) C. B. Clarke, Fl. Brit. India [J. D. Hooker] 3: 425. 1881. *Rapuntium* sect. *Isolobus* (A. DC.) Kuntze, Lex. Gen. Phan. 478. 1903. *Lobelia* subg. *Isolobus* (A. DC.) Y. S. Lian, Fl. Reipubl. Popularis Sin. 73(2): 154. 1983. TYPE [designated by J. Murata, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15: 357. 1995]: *Isolobus radicans* (Thunb.) A. DC. [= *Lobelia chinensis* Lour.].

Lobelia sect. *Hemipogon* Benth., Fl. Austral. 3: 123. 1867. TYPE [designated by J. Murata, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15: 357. 1995]: *Lobelia stenophylla* Benth.

Lobelia subsect. *Leiospermae* E. Wimm., Ann. Naturhist. Mus. Wien 56: 340. 1948. TYPE [designated by J. Murata, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15: 356. 1995]: *Lobelia dioica* R. Br.

Lobelia grex *Dioicae* E. Wimm., Ann. Naturhist. Mus. Wien 56: 340. 1948. *Lobelia* sect. *Dioicae* (E. Wimm.) J. Murata, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15: 356. 1995, as "*Dioica*." TYPE [sub Art. 22.6]: *Lobelia dioica* R. Br.

Lobelia [unranked] *Prostratae* E. Wimm., Pflanzenr. IV, 276b: 480. 1953. TYPE [here designated]: *Lobelia linnaeoides* (Hook. f.) Petrie [= *Lobelia angulata* G. Forst.].

Lobelia sect. *Paramezleria* E. Wimm., Pflanzenr. IV, 276b: 607. 1953. TYPE [sub Art. 37.3]: *Lobelia roughii* Hook. f.

Plants perennial (hemicryptophytes or geophytes) or less often annual, 2–40 cm tall; a few species dioecious. Stems gracile, herbaceous, commonly prostrate, radicant, or caespitose, rarely decumbent or ascending. Leaves commonly small, petiolate or rarely sessile; lamina typically not much longer than wide, variously rounded at apex and base; margin coarsely toothed or shallowly lobed. Flowers solitary in the axils of the upper leaves or very rarely these reduced in size, creating a terminal raceme (rarely corymbose); pedicels ebracteolate or less often bibracteolate. Corolla sub-bilabiate (unilabiate in *Lobelia chinensis*), 2–12(–15) mm, blue, purple, magenta, pink, or white; tube dorsally cleft to base (less often to middle or rarely entire), straight or nearly so; lobes monomorphic (rarely becoming somewhat dimorphic), almost as long as the tube to longer than the tube, spreading. Staminal column exserted, sometimes adnate to the corolla tube; anthers with a single long bristle on the apex of each ventral anther, often also bearded with tufts of shorter filiform hairs, very rarely all nude. Fruit a capsule or fleshy berry. Seeds ovoid to oblong, terete (rarely slightly compressed); testa reticulate (Murata type B).

Chromosome numbers. $2n = 12$, 14, 28, 42, 56, 70, 77, 84, 91, 140 (Lammers, 1993; Stace & James, 1996; Murray et al., 2004).

Distribution. Amphi-Pacific, largely in the Southern Hemisphere, with 43 species in four disjunct regions: (1) Southern and eastern Asia: India to Japan, the Ryukyu Islands, Taiwan, the Philippines, and New Guinea. Included species: *Lobelia archboldiana* (Merr. & L. M. Perry) Moeliono, *L. brachyantha* Merr. & L. M. Perry, *L. chinensis* Lour., *L. conferta* Merr. & L. M. Perry, *L. donanensis* P. Royen, *L. loochooensis* Koidz., *L. nummularia* Lam., *L. victoriensis* P. Royen. (2) Australia. Included species: *L. arnhemiaca* E. Wimm., *L. australiensis* Lammers, *L. beaugleholei* Albr., *L. benthamii* F. Muell., *L. concolor* R. Br., *L. darlingensis* (E. Wimm.) Albr., *L. dioica* R. Br., *L. gelida* F. Muell., *L. humistrata* F. Muell. ex F. M. Bailey, *L. irrigua* R. Br., *L. leucotos* Albr., *L. membranacea* R. Br., *L. mezlerioides* E. Wimm., *L. pedunculata* R. Br., *L. platycalyx* (F. Muell.) F. Muell., *L. pratioides* Benth., *L. purpurascens* R. Br., *L. quadrangularis* R. Br., *L. stenophylla* Benth., *L. surrepens* Hook. f. (3) New Zealand. Included species: *L. angulata* G. Forst., *L. arenaria* (Hook. f.) Heenan & de Lange, *L. carens* Heenan, *L. fatiscens* Heenan, *L. fugax* Heenan, Courtney & P. N. Johnson, *L. glaberrima* Heenan, *L. ionantha* Heenan, *L. linnaeoides* (Hook. f.) Petrie, *L. macrodon* (Hook. f.) Lammers, *L. perpusilla* Hook. f., *L. roughii* Hook. f. (4) Southern South America: Bolivia and southeastern Brazil to Tierra del Fuego and the Falkland Islands. Included species: *L. hederacea* Cham., *L. oligophylla* (Wedd.) Lammers, *L. pratiana* Gaudich. ex Lammers, *L. reniformis* Cham.

Discussion. This section plus the next two would be essentially equivalent to Murata's (1995) *Lobelia* subg. *Mezleria*, differing in (1) removal of *L. gibbosa* and its allies as *Lobelia* sect. *Holopogon*; (2) removal of *L. gilletii* to *Lobelia* sect. *Stenotium*; and (3) inclusion of *Hypsela*, which brings with it the name with priority (Chiapella, 1996; Lammers, 1999a). In Wimmer's (1943, 1953, 1968) system, however, the species included here were scattered among *Hypsela*, *Lobelia* sect. *Isolobus*, *Lobelia* sect. *Paramezleria*, two different greges within *Lobelia* subsect. *Leiospermae*, and *Pratia* sect. *Pratia*.

Recent molecular studies (Knox et al., 2006, 2008a; Antonelli, 2008; Heenan et al., 2008) support the circumscription used here. These studies also make it clear that most of the species of *Isotoma* (but not its type, which is allied to *Lobelia* sect.

Holopogon; see above) should likewise be included here. However, 13 of the 15 taxa affected have no available name in *Lobelia* (*L. fluviatilis* R. Br. and *L. scapigera* R. Br. are the exceptions), so they are left in *Isotoma* for the present. Conversely, the four species recently described from New Zealand, which form a clade sister to *I. fluviatilis* (R. Br.) F. Muell. ex Benth., have no names in that genus and so are listed here.

8. Lobelia sect. **Mezleriopsis** Lammers, sect. nov. TYPE: *Lobelia sonderiana* (Kuntze) Lammers.

Sectio a ceteris sectionibus *Lobeliae* corolla sub-bilabiata parva lobis plus minusve aequabilibus, antheris ventralibus apice setiferis et seminibus ellipsoideis vel oblongis testa subtiliter striata (typo D Muratae) distinguenda.

Plants annual or less often perennial (hemicryptophytes), 2–20 cm tall. Stems gracile, herbaceous, decumbent, caespitose or radicant. Leaves sessile or petiolate. Flowers solitary in the axils of the upper leaves or these reduced in size, creating a lax terminal raceme; pedicels ebracteolate or bibracteolate below the middle. Hypanthium sometimes distended ventrally; calyx lobes sometimes only 4. Corolla 1–5(–7) mm, sub-bilabiate, blue, purple, pink, or white; tube straight, cleft almost to its base on the dorsal side; lobes monomorphic, almost as long as the tube to longer than the tube, spreading, the dorsal pair nearly distinct from the trifid lip, sometimes with a crescent-shaped palate on the ventral lip at the mouth of the tube. Staminal column exserted; anthers with a single bristle (sometimes also with tufts of filiform hairs) at apex of each of the ventral pair. Fruit a capsule. Seeds ellipsoid to oblong, terete; testa striate (Murata type D).

Chromosome number. Unknown (Lammers, 1993).

Distribution. Nearly endemic to the Cape Provinces of South Africa, with *Lobelia sonderiana* extending north to Kenya; seven species. Included species: *Lobelia dodiana* E. Wimm., *L. filicaulis* (C. Presl) Schönland, *L. limosa* (Adamson) E. Wimm., *L. nugax* E. Wimm., *L. quadrisepala* (R. D. Good) E. Wimm., *L. sonderiana* (Kuntze) Lammers, *L. zwartkopensis* E. Wimm.

Discussion. This section is essentially identical in circumscription to Wimmer's (1953, 1968) *Lobelia* sect. *Mezleria*. Because the names *Mezleria* and *Lobelia* sect. *Eumezleria* are typified by a species of *Monopsis* (Lammers, 1999b, 2007a), however, they cannot be applied to this taxon. In coining the new name, an epithet reminiscent of them has been selected.

There is no equivalent taxon in Murata's (1995) classification; these species were simply included in his *Lobelia* sect. *Pratia*. It might have been possible here to parallel his approach by including these species in *Lobelia* sect. *Hypsela*, but it was felt that the differences in habit, seed coat, and biogeography made the recognition of a separate section useful. This decision is strongly supported by Antonelli's (2008) cladogram, in which the type species is sister to clades 3 to 8, while the exemplars of *Lobelia* sect. *Hypsela* constitute clade 7.

Practical references. An excellent illustration of the type species is provided by Thulin (1984: fig. 4), under the name *Lobelia angolensis* Engl. & Diels.

9. Lobelia sect. **Jasionopsis** Lammers, sect. nov. TYPE: *Lobelia jasionoides* (A. DC.) E. Wimm.

Sectio a ceteris sectionibus *Lobeliae* inflorescentia ex racemo corymboso vel subumbellato constante, corolla unilabiata parva lobis plus minusve aequabilibus transverse signatis, antheris ventralibus apice setiferis et seminibus ovoideis testa reticulata (typo B Muratae) distinguenda.

Plants annual or perennial (hemicryptophytes), 10–30 cm tall. Stems gracile, herbaceous, decumbent or ascending. Leaves sessile toward apex, petiolate below. Flowers in a terminal corymbose or subumbellate raceme; pedicels bibracteolate at base. Corolla 4–5 mm, unilabiate, pink or white with several transverse red or purple marks on each lobe; tube straight, cleft almost to its base; lobes monomorphic, almost as long as the tube to longer than the tube, deflexed. Staminal column exserted; anthers with a single apical bristle and a tuft of shorter filiform hairs on each of the ventral pair. Fruit a capsule. Seeds ovoid, terete; testa reticulate (Murata type B).

Chromosome number. Unknown (Lammers, 1993).

Distribution. Endemic to the Cape Provinces of South Africa; monotypic. Included species: *Lobelia jasionoides* (A. DC.) E. Wimm.

Discussion. In Wimmer's (1953, 1968) classification, this species and Asian *Lobelia chinensis* were the sole members of *Lobelia* sect. *Isolobus*. In light of the demonstrated geographic coherence of most lobelioid lineages (Knox et al., 2006, 2008a, 2008b; Antonelli, 2008), one might suspect that such a taxon was biphyletic. The suite of low habit,

monomorphic corolla lobes, awned ventral anthers, and reticulate testa that characterize both species is matched by the members of *Lobelia* sect. *Hypsela* and (except for the testa) *Lobelia* sect. *Mezleriopsis*. The primary character that distinguished *L. jasionoides* and *L. chinensis* from those taxa, which was used by Wimmer to unite them as *Lobelia* sect. *Isolobus*, was their unilabiate corolla. In light of biogeography and the other morphological features, I hypothesize that this was a parallelism and not a synapomorphy: the unilabiate species *L. chinensis* and *L. jasionoides* arose independently from the sub-bilabiate species of *Lobelia* sect. *Hypsela* and *Lobelia* sect. *Mezleriopsis*, respectively.

Lobelia chinensis is similar enough to sympatric *Lobelia* sect. *Hypsela* to include it therein (a move supported by molecular phylogeny [Antonelli, 2008]). However, *L. jasionoides* differs from sympatric *Lobelia* sect. *Mezleriopsis* in enough features (inflorescence type, corolla structure and pigmentation, seed morphology) that it is desirable to segregate it as a monotypic section. Because of Murata's (1995) choice of *L. chinensis* as the lectotype of *Lobelia* sect. *Isolobus*, it is not possible to use that name for a section that only includes *L. jasionoides*.

Practical references. An excellent color illustration of the sole species is provided by Sims (1826), under the name *Lobelia corymbosa* Hook. ex Graham.

10. Lobelia sect. **Tylomium** (C. Presl) Benth., Gen. Pl. [Bentham & Hooker f.] 2: 552. 1876. *Tylomium* C. Presl, Prodr. Monogr. Lobel. 31. 1836. *Tupa* sect. *Tylomium* (C. Presl) A. DC., Prodr. (DC.) 7: 394. 1839. *Rapuntium* sect. *Tylomium* (C. Presl) Kuntze, Lex. Gen. Phan. 478. 1903. TYPE [designated by Pfeiffer, Nomencl. Bot. 2: 1515. 1874]: *Lobelia assurgens* L.

Plants perennial (hemicryptophytes or chamaephytes) or shrubs, (0.3–)1–4 m tall. Stems robust, herbaceous, suffruticose, or woody, ascending or erect, simple to branched, sometimes apically rosulate. Leaves sessile or more commonly petiolate. Flowers in a terminal raceme; pedicels bibracteolate, often conspicuously so, usually near or above the middle, or rarely ebracteolate. Corolla sub-bilabiate (rarely unilabiate), magenta, pink, red, orange, yellow, green, or white, concolorous, 10–40(–57) mm; tube curved or arcuate, sometimes laterally fenestrate; lobes as long as the tube or longer, spreading. Anthers bearded with tufts of filiform hairs at apex of the ventral pair or rarely all 5. Fruit a capsule or berry. Seeds globose, ovoid, or ellipsoid, terete or rarely compressed; testa reticulate (Murata type E).

Chromosome numbers. $2n = 14, 28$ (Lepper, 1979, 1980, 1982; Lammers, 1993).

Distribution. Thirty-eight species endemic to North America, in three discrete areas: (1) Greater Antilles: Cuba, Jamaica, Hispaniola, Isla de Mona, Puerto Rico (chromosome numbers: $2n = 14, 28$). Included species: *Lobelia acuminata* Sw., *L. alticaulis* Proctor, *L. assurgens* L., *L. cacuminis* Britton & P. Wilson, *L. caledoniana* C. D. Adams, *L. caudata* (Griseb.) Urb., *L. christii* Urb., *L. cubana* Urb., *L. fawcettii* Urb., *L. grandifolia* Britton, *L. harrisii* Urb., *L. hotteana* Judd & Skean, *L. imberbis* (Griseb.) Urb., *L. innominata* Rendle, *L. martagon* (Griseb.) Hitchc., *L. oxyphylla* Urb., *L. portoricensis* (Vatke) Urb., *L. robusta* Graham, *L. rotundifolia* Juss. ex A. DC., *L. salicina* Lam., *L. shaferi* Urb., *L. viridiflora* McVaugh, *L. vivaldii* Lammers & Proctor. (2) Lesser Antilles: St. Kitts, Nevis, Montserrat, Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent, Grenada. Included species: *L. brigittalis* E. H. L. Krause, *L. cirsiifolia* Lam., *L. conglobata* Lam., *L. digitalifolia* (Griseb.) Urb., *L. kraussii* Graham, *L. persicifolia* Lam., *L. santa-luciae* Rendle, *L. stricta* Sw. (3) Southern Mexico to Panama. Included species: *L. calochlamys* (Donn. Sm.) Wilbur, *L. dressleri* Wilbur, *L. guatemalensis* (B. L. Rob. ex Donn. Sm.) Wilbur, *L. nubicola* McVaugh, *L. parvidentata* L. O. Williams, *L. tatea* (E. Wimm.) E. Wimm., *L. zelayensis* Wilbur.

Discussion. Wimmer (1943, 1953, 1968) assigned these species to two disparate taxa. Those with capsular fruit constituted the "§ species antillanae" of *Lobelia* subsect. *Primanae*, while those with indehiscent fruit were included among the members of *Pratia* sect. *Colensoa* (see above). Murata (1995) merely suggested in passing that these species "may be attributable to sect. *Homochilus*." The molecular phylogeny of Antonelli (2008) largely supported the recognition of this taxon, as four exemplars belonged to one subclade within his clade 5. *Lobelia rotundifolia*, however, fell among the exemplars of *Lobelia* sect. *Lobelia* in another subclade of clade 5. It is of interest in this regard that McVaugh (1943) earlier assigned *L. rotundifolia* to *Lobelia* sect. *Lobelia* on the basis of its fenestrate corolla and inconspicuous basal bracteoles. The name of this section would be unaffected by the addition of the genus *Hippobroma* (cf. Antonelli, 2008).

Practical references. The members of the Mexican and Central American subgroup may be identified using the key provided by Wilbur (1991).

11. Lobelia sect. **Homochilus** A. DC., Prodr. (DC.) 7: 383. 1839. *Rapuntium* sect. *Homochilus* (A. DC.) Kuntze, Lex. Gen. Phan. 478. 1903. TYPE [designated by J. Murata, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15: 369. 1995]: *Lobelia laxiflora* Kunth.

Plants perennial (hemicryptophytes or chamaephytes) or shrubs, (0.2–)0.5–3 m tall. Stems robust, herbaceous, suffruticose, or woody, ascending or erect, simple to branched. Leaves sessile or less often petiolate. Flowers solitary in the axils of the upper leaves or these reduced in size, creating a terminal raceme; pedicels ebracteolate or bibracteolate. Corolla bilabiate or sub-bilabiate (rarely unilabiate), magenta, purple, red, pink, orange, or yellow, concolorous or sharply bicolorous, 22–48(–56) mm; tube straight, laterally fenestrate or entire; lobes much shorter than the tube, spreading (rarely deflexed). Anthers bearded with tufts of filiform hairs at apex on the ventral pair. Fruit a capsule. Seeds ellipsoid or oblong, terete; testa striate (Murata type D).

Chromosome number. $2n = 14$ (Lammers, 1993).

Distribution. Endemic to the New World, with five species from southern Arizona to southwestern Colombia, and *Lobelia decurrens* endemic to Peru. Included species: *L. aguana* E. Wimm., *L. decurrens* Cav., *L. ghiesbreghtii* Decne., *L. guerrerensis* Eakes & Lammers, *L. heteroclita* McVaugh, *L. laxiflora* Kunth.

Discussion. The circumscription used here is identical to that of Wimmer (1953, 1968), Murata (1995), and Lammers (2004), and is supported by the phylogeny of Antonelli (2008).

Practical references. A key to these species and complete descriptions are provided by Lammers (2004).

12. Lobelia sect. **Tupa** (G. Don) Benth., Gen. Pl. [Bentham & Hooker f.] 2: 552. 1876. *Tupa* G. Don, Gen. Hist. 3: 700. 1834. *Lobelia* [unranked] *Tupa* (G. Don) Heynh., Nomencl. Bot. Hort. 1: 473. 1840. *Rapuntium* sect. *Tupa* (G. Don) Kuntze, Lex. Gen. Phan. 478. 1903. *Lobelia* subg. *Tupa* (G. Don) E. Wimm., Ann. Naturhist. Mus. Wien 56: 364. 1948. TYPE [sub Art. 22.6]: *Lobelia tupa* L.

Tupa sect. *Eutupa* A. DC., Prodr. (DC.) 7: 391. 1839, nom. invalid. sub Art. 21.3. *Lobelia* sect. *Eutupa* A. DC. ex E. Wimm., Ann. Naturhist. Mus. Wien 56: 365. 1948, nom. illeg. sub Art. 52.1. *Lobelia* subsect. *Primanae* E. Wimm., Ann. Naturhist. Mus. Wien 56: 365. 1948. TYPE [sub Art. 22.6]: *Lobelia tupa* L.

Plants perennial (hemicryptophytes or chamaephytes) or shrubs (rarely trees), 0.5–4(–6.8) m tall. Stems robust, herbaceous, suffruticose, or woody, ascending or erect, simple to much branched; latex white, pale yellow, or tan. Leaves sessile. Flowers solitary in the axils of the upper leaves or these reduced in size, creating a terminal raceme; pedicels ebracteolate or bibracteolate. Corolla unilabiate, red, pink, or purple, rarely yellow, concolorous or subtly bicolorous, 15–65 mm; tube arcuate; lobes much shorter than the tube, deflexed, coherent at apex. Anthers bearded with tufts of filiform hairs at apex of ventral pair. Fruit a capsule. Seeds ovoid, ellipsoid, or oblong, terete; testa striate (Murata type D).

Chromosome number. $2n = 42$ (Lammers, 1993).

Distribution. Endemic to central Chile; four species. Included species: *Lobelia bridgesii* Hook. & Arn., *L. excelsa* Bonpl., *L. polyphylla* Hook. & Arn., *L. tupa* L.

Discussion. The narrow circumscription embraced here is identical to that of Murata (1995) and Lammers (2000), which finds strong support in the molecular phylogenies of Knox et al. (1993, 2008b), Knox and Palmer (1998), Koopman and Ayers (2005), and Antonelli (2008). Wimmer's (1953, 1968) circumscription of the section was much broader, encompassing the species here treated as *Lobelia* sect. *Speirema*, *Lobelia* sect. *Trimeris*, and *Lobelia* sect. *Tylomium*, as well as some of those in *Lobelia* sect. *Rhynchopetalum*. The circumscription used here is equivalent to the "§ species chilenses" within his *Lobelia* subsect. *Primanae*.

Practical references. A key to these species and complete descriptions are provided by Lammers (2000).

13. Lobelia sect. **Trimeris** (C. Presl) A. DC., Prodr. (DC.) 7: 357. 1839. *Trimeris* C. Presl, Prodr. Monogr. Lobel. 46. 1836. *Rapuntium* sect. *Trimeris* (C. Presl) Kuntze, Lex. Gen. Phan. 478. 1903. TYPE [sub Art. 37.3]: *Trimeris*

oblongifolia C. Presl [= *Lobelia scaevolifolia* Roxb.].

Shrubs, 1–2 m tall. Stems robust, woody, decumbent or ascending, branched. Leaves petiolate. Flowers solitary in the axils of the upper leaves; pedicels ebracteolate. Corolla sub-bilabiate, white, 12–15 mm; tube slightly curved; lobes as long as the tube or longer, spreading. Anthers bearded with tufts of filiform hairs at apex of ventral pair. Fruit a capsule. Seeds ovoid, terete; testa striate-reticulate (Murata type C).

Chromosome number. Unknown (Lammers, 1993).

Distribution. Endemic to St. Helena; monotypic. Included species: *Lobelia scaevolifolia* Roxb.

Discussion. Wimmer (1953, 1968) included this species among the "§ Barbiferae–Longipedicellatae" within his *Lobelia* subsect. *Haynaldianae*. Murata (1995) did not include the species in *Lobelia*, presumably following Mabberley (1974), who accorded it generic rank.

Practical references. A detailed description of the sole species was provided by Mabberley (1974).

14. Lobelia sect. **Speirema** (Hook. f. & Thomson) Lammers, J. Bot. Res. Inst. Texas 4: 161. 2010. *Speirema* Hook. f. & Thomson, J. Proc. Linn. Soc., Bot. 2: 27. 1858. *Pratia* sect. *Speirema* (Hook. f. & Thomson) Baill., Hist. Pl. 8: 366. 1885. TYPE [sub Art. 37.3]: *Speirema montanum* (Reinw. ex Blume) Hook. f. & Thomson [≡ *Lobelia montana* Reinw. ex Blume].

Lobelia subsect. *Haynaldianae* E. Wimm., Ann. Naturhist. Mus. Wien 56: 366. 1948. TYPE [designated by J. Murata, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15: 358. 1995]: *Lobelia omeiensis* E. Wimm. [= *Lobelia fangiana* (E. Wimm.) S. Y. Hu]. [Although Mabberley (1974) earlier designated *Lobelia fistulosa* Vell., that species was not among those included in the protologue.]

Plants perennial (hemicryptophytes or chamaephytes) or shrubs, 0.3–2 m tall. Stems robust, herbaceous, suffruticose, or woody, erect, arching, straggling, or sprawling, branched or unbranched. Leaves sessile or petiolate. Flowers solitary in the axils of little-reduced or unreduced leaves (rarely the uppermost aggregated into a terminal 10- to 25-flowered raceme); pedicels ebracteolate (rarely with a pair of linear bracteoles 6–18 mm long in the lower third). Corolla sub-bilabiate, greenish, bluish lilac, red-purple, or dark violet, the lip often contrastingly striped or spotted, 12–26 mm; tube straight; lobes as long as the tube or longer, spreading. Ventral anthers bearded at apex with tufts of filiform hairs. Fruit a berry. Seeds cuboidal or quadrate, subterete or slightly compressed; testa striate-reticulate (Murata type C).

Chromosome number. Unknown (Lammers, 1993).

Distribution. Endemic to southeastern Asia, from northeastern India and Tibet to northern Vietnam, with disjunct populations of *Lobelia montana* on the Malay Peninsula, Sumatra, and Java; five species. Included species: *L. brevisepala* (Y. S. Lian) Lammers, *L. fangiana* (E. Wimm.) S. Y. Hu, *L. longipedicellata* C. E. C. Fisch., *L. montana* Reinw. ex Blume, *L. reflexisepala* Lammers.

Discussion. The members of this section were assigned to *Lobelia* sect. *Colensoa* by Murata (1995) and (as *Pratia* sect. *Colensoa*) Wimmer (1943, 1953, 1968). As noted above, the species included in that section by these authors were quite heterogeneous, belonging to disparate lineages. None of the five assigned here have been included in a phylogenetic analysis as yet, but they do form a morphologically distinctive group on the basis of their solitary axillary flowers and indehiscent fruit.

15. Lobelia sect. **Plagiobotrys** Lammers, J. Bot. Res. Inst. Texas 4: 172. 2010. TYPE: *Lobelia borneensis* (Hemsl.) Moeliono.

Plants perennial (hemicryptophytes or chamaephytes) or shrubs, 0.7–3 m tall. Stems robust, herbaceous or suffruticose, branched, sprawling or scrambling. Leaves petiolate. Flowers in a terminal pedunculate bracteate raceme that appears axillary due to overtopping by a vegetative branch; pedicels bibracteolate below the middle. Corolla sub-bilabiate, white, purple or red-purple, red, or white, 10–28 mm; tube straight; lobes longer than the tube, reflexed. Anthers with tufts of flattened hairs at apex of all 5. Fruit a fleshy purple berry. Seeds cuboidal or quadrate; testa reticulate (Murata type B).

Chromosome number. Unknown (Lammers, 1993).

Distribution. Endemic to Malesia, on Borneo, Sulawesi, and Flores; monotypic. Included species: *Lobelia borneensis* (Hemsl.) Moeliono.

Etymology. From the Greek πλαγος (meaning "placed sideways") and βοτρυς (meaning "a bunch of grapes"), in allusion to the pedunculate pseudoaxillary racemes of small purple berries.

Discussion. As with the preceding section, previous authors (Wimmer, 1943, 1953, 1968; Murata, 1995) assigned this species to *Lobelia* sect. *Colensoa*. It might be included in the preceding section on the basis of its baccate fruit, but differs conspicuously in its pseudoaxillary raceme, flattened trichomes at apex of all five anthers, and reticulate seed coat.

16. Lobelia sect. **Rhynchopetalum** (Fresen.) Benth., Gen. Pl. [Bentham & Hooker f.] 2: 552. 1876. *Rhynchopetalum* Fresen., Flora 21: 603. 1838. *Tupa* sect. *Rhynchopetalum* (Fresen.) A. Rich., Tent. Fl. Abyss. 2: 9. 1850. TYPE [sub Art. 37.3]: *Rhynchopetalum montanum* Fresen. [≡ *Lobelia rhynchopetalum* Hemsl.].

Haynaldia Kanitz, Magyar Növényt. Lapok 1: 3. 1877, nom. illeg. sub Art. 53.1, non *Haynaldia* Schur, Enum. Pl. Transsilv. 807. 1866, nec *Haynaldia* Schulzer, Verh. K.K. Zool.-Bot. Ges. Wien 16: 37. 1866. *Euhaynaldia* Borbás, Földmüv. Érdek. 8: 331. 1880. *Lobelia* sect. *Euhaynaldia* (Borbás) Zahlbr., Videnskab. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1895: 69. 1895. *Rapuntium* sect. *Haynaldia* Kuntze, Lex. Gen. Phan. 478. 1903, nom. illeg. sub Art. 52.1. TYPE [designated by Lammers, World Checkl. & Bibliogr. Campanulaceae: 348. 2007]: *Haynaldia exaltata* (Pohl) Kanitz [≡ *Lobelia exaltata* Pohl].

Lobelia ser. *Longisepalae* E. A. Bruce, Bull. Misc. Inform. Kew 1934: 63. 1934, as "*Longisepala*." TYPE [sub Art. 22.6]: *Lobelia longisepala* Engl. [The orthography of this and the following four taxa have been corrected under Article 32.7 to comply with Article 21.2.]

Lobelia ser. *Mildbraediorum* E. A. Bruce, Bull. Misc. Inform. Kew 1934: 65. 1934, as "*Mildbraedii*." TYPE [sub Art. 22.6]: *Lobelia mildbraedii* Engl.

Lobelia ser. *Giberroa* E. A. Bruce, Bull. Misc. Inform. Kew 1934: 65. 1934. TYPE [sub Art. 22.6]: *Lobelia giberroa* Hemsl.

Lobelia ser. *Deckeniorum* E. A. Bruce, Bull. Misc. Inform. Kew 1934: 65. 1934, as "*Deckenii*." TYPE [sub Art. 22.6]: *Lobelia deckenii* (Asch.) Hemsl.

Lobelia ser. *Telekiorum* E. A. Bruce, Bull. Misc. Inform. Kew 1934: 65. 1934, as "*Telekii*." TYPE [sub Art. 22.6]: *Lobelia telekii* Schweinf.

Lobelia [unranked] *Barbiferae* E. Wimm., Pflanzenr. IV, 276b: 633. 1953. TYPE [here designated]: *Lobelia organensis* Gardner.

Lobelia [unranked] *Longipedicellatae* E. Wimm., Pflanzenr. IV, 276b: 633. 1953. TYPE [here designated]: *Lobelia organensis* Gardner.

Lobelia [unranked] *Brevipedicellatae* E. Wimm., Pflanzenr. IV, 276b: 634. 1953. TYPE [here designated]: *Lobelia pyramidalis* Wall.

Lobelia [unranked] *Imberbes* E. Wimm., Pflanzenr. IV, 276b: 636. 1953. *Lobelia* subg. *Imberbes* (E. Wimm.) T. Yamaz., Fl. Japan (Iwatzuki et al., eds.) 3a: 417. 1993. *Lobelia* sect. *Imberbes* (E. Wimm.) T. Yamaz., Fl. Japan (Iwatzuki et al., eds.) 3a: 417. 1993. TYPE [designated by T. Yamaz. in K. Iwatsuki et al., Fl. Japan 3a: 417. 1993]: *Lobelia boninensis* Koidz.

Lobelia subsect. *Nicotianifoliae* Mabb., Kew Bull. 29: 561. 1974. TYPE [designated by the author]: *Lobelia nicotianifolia* Roth ex Schult.

Lobelia subsect. *Rueppellianae* Mabb., Kew Bull. 29: 571. 1974. TYPE [designated by the author]: *Lobelia rhynchopetalum* Hemsl.

Plants perennial or pliestesial (hemicryptophytes, chamaephytes, or herbaceous phanerophytes), shrubs, treelets, or trees, 0.5–9 m tall. Stems robust, typically pachycaul, herbaceous, suffruticose, or woody, prostrate, decumbent, ascending, or erect, simple, often apically rosulate. Leaves sessile (very rarely petiolate). Flowers in a terminal raceme or panicle; pedicels ebracteolate or bibracteolate. Corolla sub-bilabiate or unilabiate, various shades of blue, purple, red, yellow, green, or white, (12–)22–50 mm; tube curved or arcuate; lobes spreading or deflexed, as long as the tube or longer. Anthers bearded with tufts of filiform hairs at apex of ventral pair or all anthers nude at apex. Fruit a capsule. Seeds ovoid, lenticular, commonly winged; testa striate-reticulate (Murata type C).

Chromosome number. $2n = 28$ (Knox & Kowal, 1993; Lammers, 1993; Ruas et al., 2001).

Distribution. Almost pantropical, with 61 species in three disjunct areas: (1) Southern and eastern Asia: Sri Lanka and India to eastern China, the Bonin Islands, Taiwan, the Philippines, Vietnam, and Sumatra, with *Lobelia sessilifolia* extending north to eastern Siberia, the Russian Far East, the Kuril Islands, Korea, and Japan (chromosome number: $2n = 28$). Included species: *L. beddomeana* E. Wimm., *L. boninensis* Koidz., *L. clavata* E. Wimm., *L. colorata* Wall., *L. davidii* Franch., *L. doniana* Skottsb., *L. erectiuscula* H. Hara, *L. eryliae* C. E. C. Fisch., *L. foliiformis* T. J. Zhang & D. Y. Hong, *L. iteophylla* C. Y. Wu, *L. leschenaultiana* (C. Presl) Skottsb., *L. melliana* E. Wimm., *L. mishmica* C. B. Clarke, *L. nicotianifolia* Roth ex Schult., *L. nubigena* J. Anthony, *L. philippinensis* Skottsb., *L. pleotricha* Diels, *L. proctorii* Argent & P. Wilkie, *L. pyramidalis* Wall., *L. rosea* Wall., *L. seguinii* H. Lév. & Vaniot, *L. sessilifolia* Lamb., *L. sumatrana* Merr., *L. tibetica* W. L. Zheng. (2) Tropical Africa: Ethiopia to Transvaal and Angola, west to the Gulf of Guinea (chromosome number: $2n = 28$). Included species: *L. aberdarica* R. E. Fr. & T. C. E. Fr., *L. acrochilus* (E. Wimm.) E. B. Knox, *L. bambusetii* R. E. Fr. & T. C. E. Fr., *L. barnsii* Exell, *L. bequaertii* De Wild.,

L. burttii E. A. Bruce, *L. columnaris* Hook. f., *L. deckenii* (Asch.) Hemsl., *L. giberroa* Hemsl., *L. gregoriana* Baker f., *L. longisepala* Engl., *L. lukwangulensis* Engl., *L. mildbraedii* Engl., *L. morogoroensis* Knox & Pócs, *L. petiolata* Hauman, *L. rhynchopetalum* Hemsl., *L. ritabeaniana* E. B. Knox, *L. sancta* Thulin, *L. stricklandiae* Gilliland, *L. stuhlmannii* Schweinf. ex Stuhlmann, *L. telekii* Schweinf., *L. thuliniana* E. B. Knox, *L. udzungwensis* Thulin, *L. wollastonii* Baker f., *L. xongorolana* E. Wimm. (3) South America: southeastern Brazil, with *L. hassleri* extending into adjacent Argentina and Paraguay (chromosome number: $2n = 28$). Included species: *L. brasiliensis* A. O. S. Vieira & G. J. Sheph., *L. exaltata* Pohl, *L. fistulosa* Vell., *L. glazioviana* Zahlbr., *L. hassleri* Zahlbr., *L. hilaireana* (Kanitz) E. Wimm., *L. imperialis* E. Wimm., *L. langeana* Dusén, *L. organensis* Gardner, *L. santos-limae* Brade, *L. stellfeldii* R. Braga, *L. thapsoidea* Schott ex Pohl.

Discussion. This section is circumscribed more broadly than it was by Wimmer (1953, 1968) and Murata (1995), as it also encompasses species that the former assigned to *Lobelia* subsect. *Haynaldianae* and that the latter assigned to *Lobelia* sect. *Colensoa*. The monophyly of the section as here circumscribed is supported by the results of molecular phylogenies (Knox et al., 1993, 2006; Knox & Palmer, 1998; Antonelli, 2008).

Practical references. A key and detailed descriptions of the African representatives of the section were provided by Mabberley (1974, 1975a, 1975b).

17. Lobelia sect. **Revolutella** E. Wimm., Ann. Naturhist. Mus. Wien 56: 369. 1948. *Neowimmeria* O. Deg. & I. Deg., Phytologia 12: 73. 1965. TYPE [designated by O. Degener & I. Degener, Phytologia 12: 73. 1965]: *Lobelia grayana* E. Wimm.

Shrubs, 0.2–0.7 m tall, and treelets, 0.5–6 m tall. Stems robust, woody, prostrate or decumbent and branched (shrubs), ascending or erect and simple (treelets), sometimes apically rosulate. Leaves sessile (petiolate in extinct *Lobelia remyi* Rock). Flowers in a terminal raceme or panicle; pedicels bibracteolate near base. Corolla bilabiate, blue (treelets) or magenta (shrubs), 15–45 mm; tube straight or slightly curved; lobes as long as the tube or longer, tightly recoiled. Anthers bearded with tufts of filiform hairs at apex of ventral pair. Fruit a capsule. Seeds ellipsoid, terete; testa striate-reticulate (Murata type C).

Chromosome number. $2n = 28$ (Lammers, 1993).

Distribution. Endemic to the Hawaiian Islands, from Ni'ihau to Hawai'i; nine species. Included species: *Lobelia dunbariae* Rock, *L. grayana* E. Wimm., *L. hillebrandii* Rock, *L. hypoleuca* Hillebr., *L. monostachya* (Rock) Lammers, *L. niihauensis* H. St. John, *L. oahuensis* Rock, *L. remyi* Rock, *L. yuccoides* Hillebr.

Discussion. The circumscription used here is identical to that of Wimmer (1953, 1968), Degener and Degener (1974), Murata (1995), and Lammers (1990). Monophyly is supported by the molecular analyses of Antonelli (2008) and Givnish et al. (2009).

Practical references. A key to these species and brief descriptions are provided by Lammers (1990).

18. Lobelia sect. **Galeatella** E. Wimm., Ann. Naturhist. Mus. Wien 56: 369. 1948. *Galeatella* (E. Wimm.) O. Deg. & I. Deg., Fl. Hawaiiensis, fam. 339. 1962. TYPE [designated by O. Degener & I. Degener, Fl. Hawaiiensis, fam. 339. 1962]: *Lobelia villosa* (Rock) H. St. John & Hosaka.

Treelets, 0.7–5 m tall. Stems pachycaul, woody, ascending or erect, simple, apically rosulate. Leaves sessile; margin entire. Flowers in a terminal raceme or panicle; pedicels ebracteolate. Corolla bilabiate, pale purple, red, yellow, or white, 44–103 mm; tube straight or slightly curved; lobes as long as the tube or longer, spreading. Anthers bearded with tufts of filiform hairs at apex of all 5. Fruit a capsule. Seeds oblong, lenticular, winged; testa striate-reticulate (Murata type C).

Chromosome number. Unknown (Lammers, 1993, 2007b).

Distribution. Endemic to the Hawaiian Islands, on Kaua'i, O'ahu, Moloka'i, and Maui; five species. Included species: *Lobelia gaudichaudii* A. DC., *L. gloria-montis* Rock, *L. koolauensis* (Hosaka & Fosberg) Lammers, *L. villosa* (Rock) H. St. John & Hosaka, *L. wahiawa* Lammers.

Discussion. As with the preceding section, the circumscription used here is identical to that of Wimmer (1953, 1968), Degener and Degener (1974), Murata (1995), and Lammers (1990, 2007b). Monophyly is supported by the molecular analysis of Givnish et al. (2009). If it were to prove desirable to subsume *Trematolobelia* Zahlbr. ex Rock into this section (cf. Lammers, 2007b; Givnish et al., 2009), a

new combination based on *Rapuntium* sect. *Trematocarpus* would have priority (see below).

Practical references. A key to these species and complete descriptions are provided by Lammers (2007b).

Excluded Names

Listed here are all remaining infrageneric names that were effectively published under *Lobelia*, its later homonyms, or its homotypic synonyms. The currently accepted taxon to which the name pertains appears in brackets. Further information on typification of generic epithets serving as basionyms is provided by Lammers (2007a); and of sections of *Scaevola* (Goodeniaceae) by Carolin (1992).

Laurentia [unranked] *Hippobroma* (G. Don) Endl., Gen. Pl. 512. 1838. TYPE [sub Art. 7.4]: *Hippobroma longiflora* (L.) G. Don [≡ *Hippobroma* G. Don, Gen. Hist. 3: 17. 1834].

Laurentia sect. *Isotoma* (R. Br.) E. Wimm., Ann. Naturhist. Mus. Wien 56: 335. 1948. TYPE [sub Art. 7.4]: *Lobelia hypocrateriformis* R. Br. [≡ *Isotoma* (R. Br.) Lindl., Bot. Reg. 12: pl. 964. 1826].

Laurentia subg. *Isotoma* (R. Br.) Peterm., Pflanzenreich 444. 1845. TYPE [sub Art. 7.4]: *Lobelia hypocrateriformis* R. Br. [≡ *Isotoma* (R. Br.) Lindl., Bot. Reg. 12: pl. 964. 1826].

Laurentia [unranked] *Isotoma* (R. Br.) Endl., Gen. Pl. 512. 1838. TYPE [sub Art. 7.4]: *Lobelia hypocrateriformis* R. Br. [≡ *Isotoma* (R. Br.) Lindl., Bot. Reg. 12: pl. 964. 1826].

Laurentia sect. *Palmerella* (A. Gray) E. Wimm., Ann. Naturhist. Mus. Wien 56: 335. 1948. TYPE [sub Art. 7.4]: *Palmerella debilis* A. Gray [≡ *Palmerella* A. Gray, Proc. Amer. Acad. Arts 11: 80. 1876].

Laurentia subg. *Solenopsis* (C. Presl) Peterm., Pflanzenreich 444. 1845. TYPE [sub Art. 7.4]: *Lobelia minuta* L. [≡ *Solenopsis* C. Presl, Prodr. Monogr. Lobel. 32. 1836].

Laurentia [unranked] *Solenopsis* (C. Presl) Endl., Gen. Pl. 512. 1838. TYPE [Art. 7.4]: *Lobelia minuta* L. [≡ *Solenopsis* C. Presl, Prodr. Monogr. Lobel. 32. 1836].

Lobelia Mill., Gard. Dict. Abr., ed. 4. 1754, nom illeg. sub Art. 53.1. TYPE [sub Art. 37.3]: *Lobelia frutescens* Mill. [≡ *Scaevola* L., Mant. Pl. 2: 145. 1771, nom. cons.].

Lobelia C. Presl, Prodr. Monogr. Lobel. 33. 1836, nom. illeg. sub Art. 53.1. TYPE [designated by Lammers, World Checkl. & Bibliogr. Campanulaceae: 348. 2007]: *Lobelia westiniana* Thunb. [≡ *Siphocampylus* Pohl, Pl. Bras. Icon. Descr. 2: 104. 1831].

Lobelia [unranked] *Centropogon* (C. Presl) Heynh., Nomencl. Bot. Hort. 1: 470. 1840. TYPE [sub Art. 7.4]: *Lobelia surinamensis* L. [≡ *Centropogon* C. Presl, Prodr. Monogr. Lobel. 48. 1836].

Lobelia sect. *Crossostoma* (G. Don) Kuntze, Lex. Gen. Phan. 335. 1903. TYPE [sub Art. 7.4]: *Scaevola spinescens* R. Br. [≡ *Scaevola* L. sect. *Scaevola*].

Lobelia [unranked] *Dobrowskya* (C. Presl) Heynh., Nomencl. Bot. Hort. 1: 470. 1840, as "*Dobrowskia*." TYPE [sub Art. 7.4]: *Lobelia unidentata* W. T. Aiton [≡ *Monopsis* sect. *Dobrowskya* (C. Presl) Urb., Jahrb. Königl. Bot. Gart. Berlin 1: 271. 1881].

Lobelia sect. *Enantiophyllum* (Miq.) Kuntze, Lex. Gen. Phan. 335. 1903. TYPE [sub Art. 7.4]: *Scaevola amboinensis* Miq. [≡ *Scaevola* sect. *Enantiophyllum* Miq., Ann. Mus. Bot. Lugduno-Batavum 1: 210. 1864].

Lobelia sect. *Eumezleria* E. Wimm., Pflanzenr. IV, 276b: 602. 1953. TYPE [designated by J. Murata, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15: 357. 1995]: *Lobelia depressa* L. f. [= *Monopsis* Salisb. sect. *Monopsis*].

Lobelia [unranked] *Isotoma* R. Br., Prodr. 565. 1810. TYPE [sub Art. 37.3]: *Lobelia hypocrateriformis* R. Br. [≡ *Isotoma* (R. Br.) Lindl., Bot. Reg. 12: pl. 964. 1826].

Lobelia [unranked] *Laurentia* Heynh., Nomencl. Bot. Hort. 1: 470. 1840. TYPE [sub Art. 7.4]: *Lobelia minuta* L. [≡ *Solenopsis* C. Presl, Prodr. Monogr. Lobel. 32. 1836].

Lobelia sect. *Mezleria* (C. Presl) Schönl., Nat. Pflanzenfam. [Engler & Prantl] IV(5): 67. 1889. TYPE [sub Art. 7.4]: *Lobelia depressa* L. f. [= *Monopsis* Salisb. sect. *Monopsis*].

Lobelia subg. *Mezleria* (C. Presl) E. Wimm., Ann. Naturhist. Mus. Wien 56: 364. 1948. TYPE [sub Art. 7.4]: *Lobelia depressa* L. f. [= *Monopsis* Salisb. sect. *Monopsis*].

Lobelia [unranked] *Monopsis* (Salisb.) Heynh., Nomencl. Bot. Hort. 1: 473. 1840. TYPE [sub Art. 7.4]: *Lobelia speculum* Andrews [≡ *Monopsis* Salisb., Trans. Hort. Soc. London 2: 37. 1817].

Lobelia sect. *Palmerella* (A. Gray) McVaugh, Amer. Midl. Naturalist 24: 682. 1940. TYPE [sub Art. 7.4]: *Palmerella debilis* A. Gray [≡ *Palmerella* A. Gray, Proc. Amer. Acad. Arts 11: 80. 1876].

Lobelia [unranked] *Parastranthus* (G. Don) Heynh., Nomencl. Bot. Hort. 1: 473. 1840. TYPE [sub Art. 7.4]: *Lobelia lutea* L. [≡ *Monopsis* sect. *Xanthomeria* (C. Presl) Lammers].

Lobelia sect. *Pogonanthera* (G. Don) Kuntze, Lex. Gen. Phan. 335. 1903. TYPE [sub Art. 7.4]: *Scaevola striata* R. Br. [≡ *Scaevola* subsect. *Pogonanthera* (G. Don) Carolin, Telopea 3: 490. 1990].

Lobelia [unranked] *Siphocampylus* (Pohl) Heynh., Nomencl. Bot. Hort. 1: 473. 1840. TYPE [sub Art. 7.4]: *Siphocampylus westinianus* (Thunb.) Pohl [≡ *Siphocampylus* Pohl, Pl. Bras. Icon. Descr. 2: 104. 1831].

Laurentia subg. *Solenanthis* (Kunth) Peterm., Pflanzenreich 444. 1845. TYPE [sub Art. 7.4]: *Lobelia longiflora* L. [≡ *Hippobroma* G. Don, Gen. Hist. 3: 717. 1834].

Lobelia [unranked] *Solenanthis* Kunth, Nov. Gen. Sp. [H.B.K.] 3: 309 (quarto), 241 (folio). 1819. TYPE [sub Art. 37.3]: *Lobelia longiflora* L. [≡ *Hippobroma* G. Don, Gen. Hist. 3: 717. 1834].

Lobelia sect. *Takkada* Kuntze, Lex. Gen. Phan. 335. 1903, nom. invalid. sub Art. 22.2. [≡ *Scaevola* L. sect. *Scaevola*].

Lobelia [unranked] *Xanthomeria* (C. Presl) Endl., Gen. Pl. 512. 1838. TYPE [sub Art. 7.4]: *Rapuntium luteum* (L.) C. Presl [≡ *Monopsis* sect. *Xanthomeria* (C. Presl) Lammers].

Lobelia sect. *Xerocarpa* (G. Don) Kuntze, Lex. Gen. Phan. 335. 1903. TYPE [sub Art. 7.4]: *Scaevola crassifolia* Labill. [≡ *Scaevola* sect. *Xerocarpa* G. Don, Gen. Hist. 3: 730. 1834].

Rapuntium sect. *Grammatotheca* (C. Presl) Kuntze, Lex. Gen. Phan. 478. 1903. TYPE [sub Art. 7.4]: *Clintonia*

bergiana (Cham.) G. Don [≡ *Grammatotheca* C. Presl, Prodr. Monogr. Lobel. 43. 1836].

Rapuntium sect. *Mezleria* (C. Presl) Kuntze, Lex. Gen. Phan. 477. 1903, as "*Metzleria*." TYPE [sub Art. 7.4]: *Lobelia depressa* L. f. [= *Monopsis* Salisb. sect. *Monopsis*].

Rapuntium sect. *Monopsis* (Salisb.) Kuntze, Lex. Gen. Phan. 478. 1903. TYPE [sub Art. 7.4]: *Lobelia speculum* Andrews [≡ *Monopsis* Salisb., Trans. Hort. Soc. London 2: 37. 1817].

Rapuntium sect. *Parastranthus* (G. Don.) Kuntze, Lex. Gen. Phan. 478. 1903. TYPE [sub Art. 7.4]: *Lobelia lutea* L. [≡ *Monopsis* sect. *Xanthomeria* (C. Presl) Lammers].

Rapuntium sect. *Trematocarpus* Kuntze, Lex. Gen. Phan. 478. 1903. TYPE [sub Art. 7.4]: *Trematocarpus macrostachys* (Hook. & Arn.) Zahlbr. [≡ *Trematolobelia* Zahlbr. ex Rock, Bull. Coll. Hawaii Publ. 2: 45. 1913].

Rapuntium sect. *Xanthomeria* C. Presl, Prodr. Monogr. Lobel. 11. 1836. TYPE [here designated]: *Rapuntium luteum* (L.) C. Presl [≡ *Monopsis* sect. *Xanthomeria* (C. Presl) Lammers, comb. nov.].

This combination is effected here to provide the correct name for the taxon that Wimmer (1953, 1968) called *Monopsis* sect. *Parastranthus* (G. Don) E. Wimm. (cf. Lammers, 2007a, 2007c).

Addendum

Since this paper was submitted, three papers have appeared that change somewhat certain aspects described here:

Lammers, T. G. 2010. Revision of *Lobelia* sect. *Speirema* (Campanulaceae: Lobelioideae). J. Bot. Res. Inst. Texas. 4: 159–168.

This section now contains just four species. *Lobelia brevisepala* and *L. reflexisepala* are now included within the circumscription of *L. montana*, while *L. deleiensis* C. E. C. Fisch. (formerly placed there) is now recognized. The article includes a key to species and subspecies and full descriptions.

Lammers, T. G. 2010. Revision of *Lobelia* sect. *Plagiobotrys* (Campanulaceae: Lobelioideae). J. Bot. Res. Inst. Texas. 4: 169–180.

Lobelia origenes Lammers, newly described from Borneo, was added to this section. The article includes a key to species and subspecies and full descriptions.

Lammers, T. G. 2011. Revision of the Malesian species of *Lobelia* sect. *Rhynchopetalum* (Campanulaceae: Lobelioideae). Blumea. 56: in press.

Lobelia sulawesiensis Lammers, newly described from Sulawesi, was added to this section. The article includes a key to species and subspecies and full descriptions.

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Appendix 1. Index to sectional assignments.

This is an index to all species included within *Lobelia* by Lammers (2007a), plus those added to the genus subsequently (Argent et al., 2007; Lammers, 2007b; Heenan et al., 2008; Knox et al., 2008a; Senterre & Castillo-Campos, 2008). It will permit one to determine the section (denoted parenthetically by its number as given in the following list) to which a species of *Lobelia* was assigned in the discussion above. Names in the literature that do not appear in this index may be sought in the synonymy lists of Lammers (2007a) to determine the species to which it is currently assigned.

1. *Lobelia* sect. *Delostemon*
2. *Lobelia* sect. *Holopogon*
3. *Lobelia* sect. *Colensoa*
4. *Lobelia* sect. *Cryptostemon*
5. *Lobelia* sect. *Stenotium*
6. *Lobelia* sect. *Lobelia*
7. *Lobelia* sect. *Hypsela*
8. *Lobelia* sect. *Mezleriopsis*
9. *Lobelia* sect. *Jasionopsis*
10. *Lobelia* sect. *Tylomium*
11. *Lobelia* sect. *Homochilus*
12. *Lobelia* sect. *Tupa*
13. *Lobelia* sect. *Trimeris*
14. *Lobelia* sect. *Speirema*
15. *Lobelia* sect. *Plagiobotrys*
16. *Lobelia* sect. *Rhynchopetalum*
17. *Lobelia* sect. *Revolutella*
18. *Lobelia* sect. *Galeatella*

L. aberdarica (16), *L. acrochilus* (16), *L. acuminata* (10), *L. acutidens* (5), *L. adnexa* (5), *L. agrestis* (5), *L. aguana* (11), *L. alsinoides* (1), *L. alticaulis* (10), *L. amoena* (6), *L. anatina* (5), *L. anceps* (5), *L. andrewsii* (2), *L. angulata* (7), *L. appendiculata* (6), *L. aquaemontis* (5), *L. aquatica* (1), *L. archboldiana* (7), *L. ardisiandroides* (1), *L. arenaria* (7), *L. arnhemiaca* (7), *L. assurgens* (10), *L. aurita* (5), *L. australiensis* (7).

L. bambusetii (16), *L. barkerae* (1), *L. barnsii* (16), *L. baumannii* (1), *L. beaugleholei* (7), *L. beddomeana* (16), *L. benthamii* (7), *L. bequaertii* (16), *L. berlandieri* (5), *L. blantyrensis* (1), *L. boivinii* (5), *L. boninensis* (16), *L. borneensis* (15), *L. boykinii* (6), *L. brachyantha* (7), *L. brasiliensis* (16), *L. brevifolia* (6), *L. brevisepala* (14), *L. bridgesii* (12), *L. brigittalis* (10), *L. burttii* (16).

L. cacuminis (10), *L. caeciliae* (5), *L. caerulea* (1), *L. caledoniana* (10), *L. calochlamys* (10), *L. camporum* (5), *L. canbyi* (6), *L. capillifolia* (1), *L. cardinalis* (6), *L. carens* (7), *L. caudata* (10), *L. chamaedryifolia* (1), *L. chamaepitys* (1), *L. cheranganiensis* (5), *L. chevalieri* (1), *L. chinensis* (7), *L. chireensis* (5), *L. christii* (10), *L. circaeoides* (5), *L. cirsiifolia* (10), *L. clavata* (16), *L. cliffortiana* (5), *L. cobaltica* (1), *L. cochlearifolia* (1), *L. collina* (5), *L. colorata* (16), *L. columnaris* (16), *L. comosa* (5), *L. comptonii* (1), *L. concolor* (7), *L. conferta* (7), *L. conglobata* (10), *L. cordifolia* (5), *L. corniculata* (1), *L. coronopifolia* (1), *L. cubana* (10), *L. cuneifolia* (5), *L. cyanea* (5), *L. cymbalarioides* (5), *L. cyphioides* (5).

L. darlingensis (7), *L. dasyphylla* (1), *L. davidii* (16), *L. deckenii* (16), *L. decurrens* (11), *L. decurrentifolia* (1), *L. dentata* (2), *L. diastateoides* (5), *L. diazlunae* (5), *L. dichroma* (1), *L. dielsiana* (5), *L. digitalifolia* (10), *L. dioica* (7), *L. dissecta* (5), *L. divaricata* (5), *L. djurensis* (1), *L. dodiana* (8), *L. donanensis* (7), *L. doniana* (16), *L. dortmanna* (6), *L. dregeana* (5), *L. dressleri* (10), *L. dunbariae* (17), *L. duriprati* (5).

L. ehrenbergii (5), *L. elongata* (6), *L. endlichii* (5), *L. erectiuscula* (16), *L. erinus* (5), *L. erlangeriana* (5), *L. eryliae* (16), *L. eurypoda* (1), *L. exaltata* (16), *L. excelsa* (12), *L. exilis* (5).

L. fangiana (14), *L. fastigiata* (5), *L. fawcettii* (10), *L. feayana* (6), *L. fenestralis* (4), *L. fervens* (5), *L. filicaulis* (8), *L. filiformis* (5), *L. filipes* (5), *L. fistulosa* (16), *L. flaccida* (5), *L. flaccidifolia* (6), *L. flexicaulis* (5), *L. flexuosa* (5), *L. floridana* (6), *L. foliiformis* (16), *L. fugax* (7).

L. galpinii (5), *L. gattingeri* (6), *L. gaudichaudii* (18), *L. gelida* (7), *L. georgiana* (6), *L. ghiesbreghtii* (11), *L. gibbosa* (2), *L. giberroa* (16), *L. gilgii* (5), *L. gilletii* (5), *L. glaberrima* (7), *L. gladiaria* (5), *L. glandulosa* (6), *L. glaucescens* (5), *L. glazioviana* (16), *L. gloria-montis* (18), *L. goetzei* (1), *L. goldmanii* (5), *L. gouldii* (2), *L. gracillima* (5), *L. grandifolia* (10), *L. graniticola* (5), *L. grayana* (17), *L. gregoriana* (16), *L. griffithii* (1), *L. gruina* (5), *L. guatemalensis* (10), *L. guerrerensis* (11), *L. gypsophila* (5).

L. hainanensis (5), *L. harrisii* (10), *L. hartlaubii* (1), *L. hartwegii* (4), *L. hassleri* (16), *L. hederacea* (7), *L. henodon* (5), *L. henricksonii* (5), *L. hereroensis* (5), *L. heteroclita* (11), *L. heterophylla* (2), *L. heyneana* (5), *L. hilaireana* (16), *L. hillebrandii* (17), *L. hintoniorum* (5), *L. hirtipes* (5), *L. holotricha* (4), *L. holstii* (1), *L. homophylla* (5), *L. horombensis* (5), *L. hotteana* (10), *L. humistrata* (7), *L. humpatensis* (1), *L. hypnodes* (5), *L. hypoleuca* (17), *L. hypsibata* (5).

L. illota (5), *L. imberbis* (10), *L. imperialis* (16), *L. inconspicua* (5), *L. inflata* (6), *L. innominata* (10), *L. intercedens* (5), *L. ionantha* (7), *L. irasuensis* (4), *L. irrigua* (7), *L. iteophylla* (16).

L. jaliscensis (4), *L. jasionoides* (9).

L. kalmii (6), *L. kalobaensis* (5), *L. kirkii* (5), *L. knoblochii* (5), *L. koolauensis* (18), *L. kraussii* (10), *L. kundelungensis* (5).

L. langeana (16), *L. lasiocalycina* (5), *L. laurentioides* (5), *L. laxa* (5), *L. laxiflora* (11), *L. leichhardii* (2), *L. lepida* (5), *L. leschenaultiana* (16), *L. leucotos* (7), *L. limosa* (8), *L. linarioides* (5), *L. lindblomii* (5), *L. linearis* (1), *L. lingulata* (5), *L. linnaeoides* (7), *L. lisowskii* (5), *L. lithophila* (5), *L. livingstoniana* (5), *L. lobata* (5), *L. longicaulis* (5), *L. longipedicellata* (14), *L. longisepala* (16), *L. loochooensis* (7), *L. lucayana* (5), *L. lukwangulensis* (16), *L. luruniensis* (5), *L. luzoniensis* (5).

L. macdonaldii (4), *L. macraeana* (1), *L. macrocentron* (5), *L. macrodon* (7), *L. malowensis* (1), *L. margarita* (5), *L. martagon* (10), *L. mcvaughii* (5), *L. melliana* (16), *L. membranacea* (7), *L. mexicana* (5), *L. mezlerioides* (7), *L. microcarpa* (1), *L. mildbraedii* (16), *L. minutula* (5), *L. mishmica* (16), *L. modesta* (5), *L. molleri* (5), *L. monostachya* (17), *L. montana* (14), *L. morogoroensis* (16), *L. muscoides* (5).

L. nana (5), *L. neglecta* (1), *L. neumannii* (5), *L. nicotianifolia* (16), *L. niihauensis* (17), *L. nubicola* (10), *L. nubigena* (16), *L. nugax* (8), *L. nummularia* (7), *L. nummularioides* (1), *L. nuttallii* (6).

L. oahuensis (17), *L. obconica* (5), *L. occidentalis* (5), *L. oligophylla* (7), *L. oreas* (5), *L. organensis* (16), *L. orientalis* (5), *L. ovina* (1), *L. oxyphylla* (10).

L. paludigena (5), *L. paludosa* (6), *L. paranaensis* (5), *L. parva* (5), *L. parvidentata* (10), *L. parvisepala* (5), *L. patula* (1), *L. pedunculata* (7), *L. pentheri* (5), *L. perpusilla* (7), *L. perrieri* (5), *L. persicifolia* (10), *L. petiolata* (16), *L. philippinensis* (16), *L. physaloides* (3), *L. pinifolia* (1), *L. platycalyx* (7), *L. pleotricha* (16), *L. poetica* (4), *L. polyphylla* (12), *L. porphyrea* (5), *L. portoricensis* (10), *L. pratiana* (7), *L. pratioides* (7), *L. preslii* (1), *L. pringlei* (5), *L. proctorii* (16), *L. psilostoma* (2), *L. pteropoda* (1), *L. puberula* (6), *L. pubescens* (5), *L. pulchella* (5), *L. purpurascens* (7), *L. purpusii* (5), *L. pyramidalis* (16).

L. quadrangularis (7), *L. quadrisepala* (8), *L. quarreana* (5).

L. rarifolia (2), *L. reflexisepala* (14), *L. reinekeana* (5), *L. remyi* (17), *L. reniformis* (7), *L. reverchonii* (6), *L. rhombifolia* (2), *L. rhynchopetalum* (16), *L. rhytidosperma* (2), *L. ritabeaniana* (16), *L. rivalis* (5), *L. robusta* (10), *L. rosea* (16), *L. rotundifolia* (10), *L. roughii* (7), *L. rubescens* (5).

L. salicina (10), *L. sancta* (16), *L. santa-luciae* (10), *L. santos-limae* (16), *L. sapinii* (5), *L. sartorii* (5), *L. scaevolifolia* (13), *L. scebelii* (5), *L. schimperi* (5), *L. scrobiculata* (5), *L. seguinii* (16), *L. serpens* (5), *L. sessilifolia* (16), *L. setacea* (1), *L. shaferi* (10), *L. simplicicaulis* (2), *L. sinaloae* (4), *L. siphilitica* (6), *L. solaris* (5), *L. sonderiana* (8), *L. spathopetala* (5), *L. spicata* (6), *L. standleyi* (5), *L. stellfeldii* (16), *L. stenocarpa* (1), *L. stenodonta* (5), *L. stenophylla* (7), *L. stenosiphon* (5), *L. stolonifera* (5), *L. stricklandiae* (16), *L. stricta* (10), *L. stuhlmannii* (16), *L. sublibera* (5), *L. subnuda* (5), *L. subpubera* (5), *L. sumatrana* (16), *L. surrepens* (7), *L. sutherlandii* (5).

L. tarsophora (5), *L. tatea* (10), *L. telekii* (16), *L. telephioides* (5), *L. tenera* (5), *L. tenuior* (2), *L. terminalis* (1), *L. thapsoidea* (16), *L. thermalis* (1), *L. thuliniana* (16), *L. tibetica* (16), *L. tomentosa* (1), *L. trigonocaulis* (2), *L. tripartita* (5), *L. trullifolia* (5), *L. tupa* (12).

L. udzungwensis (16), *L. uliginosa* (5), *L. umbellifera* (4), *L. urens* (5).

L. vagans (5), *L. valida* (5), *L. vanreenensis* (1), *L. victoriensis* (7), *L. villaregalis* (5), *L. villosa* (18), *L. viridiflora* (10), *L. vivaldii* (10), *L. volcanica* (5).

L. wahiawa (18), *L. welwitschii* (5), *L. wilmsiana* (5), *L. winifrediae* (2), *L. wollastonii* (16).

L. xalapensis (5), *L. xongorolana* (16).

L. yucatana (5), *L. yuccoides* (17).

L. zelayensis (10), *L. zeylanica* (1), *L. zwartkopensis* (8).

NEWLY SEQUENCED NUCLEAR GENE (*XDH*) FOR INFERRING ANGIOSPERM PHYLOGENY[1]

Cynthia M. Morton[2]

Abstract

The nuclear gene xanthine dehydrogenase (*Xdh*) was sequenced for 247 genera representing all major lineages of angiosperms and "gymnosperms," and the results were analyzed using likelihood and parsimony methods. The overall topology is mostly congruent with previously published trees based on chloroplast *rbcL*, *atpB*, and *matK* sequences. A total of 190 of the 253 nodes (71%) of the *Xdh* tree received bootstrap support greater than 50%. The likelihood tree was comparable in robustness to the *matK* topology, which exhibited 79% of the nodes with bootstrap support greater than 50%, and to the reported 7%–24% support observed for individual analyses of *rbcL*, *atpB*, and 18S ribosomal DNA clades. The number of parsimony-informative sites (1068, 69%) was similar to that of the *matK* (1083, 62%) study. The likelihood tree depicts angiosperms as monophyletic, with *Ceratophyllum* L. (Ceratophyllaceae) as sister to the rest of the flowering plants, followed successively by Amborellaceae, Nymphaeaceae, and Austrobaileyales clades as sisters to the remaining angiosperms. *Acorus* L. plus the remaining monocots, magnoliids, and Chloranthaceae diverge after the Austrobaileyales. Eudicots are supported and include a basal grade of Ranunculales–Proteaceae, Sabiaceae, Trochodendraceae, Buxaceae, Gunneraceae, and Dilleniaceae–Santalaceae, which are subsequent sister to the remaining eudicots. The remaining eudicots are split into two clades. The first clade consists of the Ericales, Cornales, and euasterids I and II (lamids–campanulids). The second clade consists of the following orders: Saxifragales, Myrtales–Caryophyllales–Cucurbitales, Crossosomatales, Geraniales, Rosales–Fabales–Fagales, Celastrales, Malpighiales, Brassicales–Malvales, Oxalidales, and Sapindales. *Xdh* data provided good support in the Caryophyllales, Ericales and Cornales, euasterids I (lamids), Magnoliales and Laurales, Malvales, Rutaceae, Oxalidales, Brassicales, and Sapindales. A future combined analysis of *Xdh* and other DNA data sets will have a strong potential to enhance resolution and internal support for angiosperm phylogenetics and provide insights into angiosperm evolution using biparental information.

Key words: Angiosperm, nuclear, phylogeny, systematics, xanthine dehydrogenase, *Xdh*.

DNA-based phylogenetic analyses of angiosperms have made use of a number of chloroplast markers over the past 15 years (Chase et al., 1993; Angiosperm Phylogeny Group, 1998; Soltis et al., 1999, 2000, 2003, 2005, 2007b; Savolainen et al., 2000; Angiosperm Phylogeny Group II, 2003; Hilu et al., 2003; Jansen et al., 2007). More recently, the basal angiosperms have been examined using chloroplast, nuclear, and mitochondrial markers (Qiu et al., 2006). Patterns have emerged regarding relationships among the angiosperms: (1) *Amborella* Baill. or *Amborella*–Nymphaeales represents the earliest diverging lineage of extant angiosperms, with Austrobaileyales the next clade to diverge; (2) *Ceratophyllum* L. is sister to either the monocots or eudicots; (3) magnoliids are composed of four orders (Canellales, Laurales, Magnoliales, and Piperales); (4) the monocots, a well-defined group; and (5) the Ranunculales, usually the first lineage in the eudicots, with Buxaceae, Caryophyllales, Cornales, Dilleniaceae, Ericales, euasterids, Gunnerales, Proteaceae, rosids, Sabiaceae, Santalales, and Trochodendraceae following in various arrangements and forming well-supported clades (Angiosperm Phylogeny Group II, 2003; Hilu et al., 2003; Soltis et al., 2005). Not all lineages are stable in their positions on individual or combined gene trees, and many have weak support. Major clades within basal angiosperms that have varied in position include the following: *Amborella*, Austrobaileyales, *Ceratophyllum*, magnoliids, monocots, and Nymphaeaceae (Angiosperm Phylogeny Group II, 2003; Hilu et al., 2003; Soltis et al., 2003; Qiu et al., 2006; Moore et al., 2007). Moreover, the relationships among the major clades of eudicots (Caryophyllales, Cornales, Dilleniaceae, Ericales, euasterids, Proteaceae, rosids, Sabiaceae, and Santalales) remain uncertain (Angiosperm Phylogeny Group II, 2003; Hilu et al., 2003; Soltis et al., 2003; Qiu et al., 2006). Resolving these relationships is essential for systematics and for tracing character evolution. Furthermore, many other fields of study rely on a well-supported angiosperm phylogeny, so it

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is crucial that phylogenetics produce a well-resolved topology using molecular and nonmolecular features.

Studies of broad angiosperm phylogenetics have centered on using chloroplast genes individually and in combination (Chase et al., 1993; Soltis et al., 1997, 2000; Savolainen et al., 2000; Hilu et al., 2003; Jansen et al., 2007). More recently, mitochondrial genes have been incorporated into basal angiosperm phylogenies (*rpo*C2, Qiu et al., 2006). Nuclear genes have hardly been used, and only the 18S gene has been extensively incorporated into multigene analyses investigating angiosperm phylogeny (Soltis et al., 1997). On its own, 18S has provided very limited resolution and low internal support for many major clades (Soltis et al., 1997). Studies of *rbcL* and *atpB* chloroplast genes have provided phylogenies with more resolution than individual genes; however, topological incongruence does occur between the genes (Savolainen et al., 2000). Analysis of the chloroplast gene *matK* provided a tree with greater resolution and more support for major clades, but topological incongruences were observed among *matK*, *rbcL*, and *atpB*. Combining chloroplast genes in multigene data sets for analysis has improved both resolution and internal support (Savolainen et al., 2000; Burleigh et al., 2009). Hilu et al. (2003) compared bootstrap/jackknife values for major nodes within the angiosperm trees and found the following supported percentages for these genes: *rbcL* (24%), *atpB* (14%), 18S (7%), *rbcL/atpB* (55%), and *rbcL/atpB*/18S (83%). When using chloroplast genes, one must be a bit cautious because these genes are maternally inherited and, due to issues such as hybridization, the resulting phylogenetic reconstructions may not reflect the "true phylogeny" or correct topology. The first angiosperm consensus tree based on combined chloroplast (*rbcL* and *atpB*) and nuclear (18S) genes was conducted by Soltis et al. (2000). Although 18S is a very slowly evolving gene, the combined chloroplast and nuclear consensus tree may be considered the currently most reliable overall angiosperm phylogeny because it is based on both maternally and biparentally inherited genes. However, many of the interrelationships in the angiosperm and land plant phylogenies are still controversial, and it is imperative to use information from different biparentally inherited genes to clarify and enhance the results derived largely from chloroplast genes.

Xanthine dehydrogenase is a member of the molybdenum hydroxylase family of enzymes, which are thought to play important metabolic roles in purine metabolism and hormone biosynthesis. Molybdenum (Mo) is essential for (nearly) all organisms and functions in more than 40 enzymes by catalyzing diverse redox reactions. Only four of those enzymes have been found in plants: nitrate reductase; aldehyde oxidase(s); xanthine dehydrogenase, which is involved in purine catabolism and stress reactions; and sulphite oxidase (Mendel & Hänsch, 2002). Among Mo enzymes, the alignment of amino acid sequences permits the definition of domains that are well conserved, although they are variable. This study amplified approximately 1265 bp of the xanthine dehydrogenase gene (*Xdh*), which is located on chromosome 4, contig fragment no. 82, and is approximately 4083 bp long (information obtained by comparing published *Arabidopsis* and this study's sequences). The sequenced segment lies from 358 to 1623 bp including intron 1–3 and exon 2–4. The *Arabidopsis* (DC.) Heynh. sequence contains 13 introns and 14 exons. Hesberg et al. (2004) found that *Arabidopsis* has a 46%–47% identity to human and bovine *Xdh* and therefore is homologous to *Xdh* from other organisms. This examination segment contains approximately 11 indel regions. To date, only one copy of the gene has been reported, except in silkworms and *Arabidopsis*, in which a second copy has been found. In *Arabidopsis*, Hesberg et al. (2004) reported that the physicochemical properties of AtXDH1 and AtXDH2 might be nearly identical because of their high degree of sequence similarity (94%).

Markers from the nuclear genome that can be used on a broad taxonomic scale without problems of paralogy are limited in number. The possibility of paralogy exists for all genes, not just nuclear ones, because gain and loss of genes by various processes are continuous and all genes have some probability of being duplicated or lost. One consequence of paralogy is that gene trees derived from samples of single genes from each species may not match the species tree. Having more than one gene tree to compare the angiosperm phylogeny is a good indicator of having paralogous genes. We have used this test of congruence among genes to evaluate duplications or losses within *Xdh*.

This analysis provides the first angiosperm plant gene tree using *Xdh*. More recently other researchers have been exploring the utility of *Xdh* for "gymnosperm" phylogenetics and have found it to be similar to inferences using other genes and to be highly informative (Peery et al., 2008).

We compared the topology obtained from this gene to previously published topologies from *rbcL*, *atpB*, and *matK* genes. This assessment was done to achieve two major goals: (1) compare maternally inherited genes to a biparental gene to see if the topologies are more, equally, or less resolved,

supported, and congruent, and (2) examine and compare the topologies for basal angiosperms and eudicots among the data sets for a greater understanding of seed plant relationships.

Materials and Methods

TAXON SAMPLING

Several different publications were consulted for taxon sampling schemes, including Savolainen et al. (2000), Soltis et al. (2000), Hilu et al. (2003), and Qiu et al. (2006). In total, 253 species representing 164 families and 247 genera of angiosperms and gymnosperms were sampled, and all but one was sequenced specifically for this study. See Appendix 1 for a list of taxa with accession data and GenBank numbers.

DNA ISOLATION, GENE AMPLIFICATION, AND SEQUENCING

For most samples, total DNA was isolated from fresh or herbarium specimens, although some was acquired from previously extracted samples. Leaves were ground with a mortar and pestle and subsequently extracted using the DNEasy plant DNA extraction kit (Qiagen, Valencia, California, U.S.A.) following the manufacturer's protocol. Specific polymerase chain reaction (PCR) and sequencing primers were initially designed using the *Arabidopsis* plant sequences and other organisms available in GenBank and used by Rodríguez-Trelles et al. (2003). Additional primers were redesigned as needed. See Table 1 for a list of primers used for amplification and sequencing. Cloning was performed on selected taxa using the pGem T-easy vector system II kit (Promega Corporation, Madison, Wisconsin, U.S.A.) following the manufacturer's protocol. PCR was performed with 10 μmol/L primers in 25-μL reactions. In general, it was conducted using the following program: 96°C for 1 min. followed by 34 cycles of 94°C for 30–60 sec., 48°–60°C for 1 min., 68°C for 60–80 sec., and finally 72°C for 7 min. For some taxa, the initial 96°C for 1 min. and the final 72°C for 7 min. were eliminated. Primers used for amplification of clones were M13F and M13R. For sequencing reactions, the Big Dye Terminator Sequencing 3.1 kit (Applied Biosystems, Foster City, California, U.S.A.) was used, and fragments were separated on an ABI3730 DNA Analyzer from Applied Biosystems.

PHYLOGENETIC ANALYSIS

The *Xdh* gene was analyzed using both maximum parsimony (MP) and maximum likelihood (ML). For the MP analysis, a heuristic search with PAUP* (Swofford, 2004) was completed using the following strategy: addition sequence random, number of replicates 100, tree bisection-reconnection branch swapping, MULTREE option on, and MAXTREE auto-increased by 100.

For likelihood analyses, the program MODELTEST v. 3.6 (Posada & Crandall, 1998) was used to select the models of nucleotide evolution. The program GARLI v. 0.96 (Genetic Algorithm for Rapid Likelihood Inference; Zwickl, 2006) implementing the general time reversible (GTR) substitution model, with the base frequency and proportion of invariable sites estimated, was used for the *Xdh* gene data set.

The parsimony bootstrapping analyses (100 replicates) were conducted in PAUP* (Swofford, 2004) using simple taxon addition, one tree held at each step during stepwise addition, tree bisection-reconnection branch swapping, MULTREE option on, and no upper limit of MAXTREE set.

Table 1. Primers used for the amplification along with their sequences. The *Xdh* gene was split into two halves for amplification (forward and reverse). All taxa used in this study were amplified with a combination of the primers listed below, except for primer 1299-GF, which was designed to amplify the back half in gymnosperm taxa.

Primer name	Sequence
*471F	5′-CAATGTGGRTTTGTYACYCCYGG-3′
*486F	5′-ACYCCYGGKTTTRTIATGTCIATGTA-3′
497F	5′-TTGTGATGTCGATGTATGC-3′
975R	5′-TGCTCCWGCAGCCATCCAGAG-3′
*1362R	5′-TCWGATATTGGACTAGCWGT-3′
*1365R	5′-TTYAARTCHGATATYGGACTRGC-3′
*1296F	5′-AARTGGTTYGCYGGIACACARAT-3′
1299F	5′-TGGTTTGCTGGGACACAAAT-3′
1299-1F	5′-TGGTTTGCHGGSAMHCARAT-3′
1299-GF	5′-TGGTTTGCTGGVAVYCARAT-3′
*1869R	5′-CGAAAYTCMACCATTCCMCCAGG-3′
1872R	5′-CGAAAYTCMACCATTCCMCC-3′
1869-1R	5′-CKAAWYTCMACCATTCCMCCAGG-3′
1354R	5′-CAGAAACTATCCATKICCC-3′

* Amplification and sequencing primers used in more than 75% of the taxa examined.

Results

CLONES

Among plants, only *Arabidopsis* has been previously reported to have two copies of *Xdh*, and these copies have a high degree of similarity (94%). Hesberg et al. (2004) reported that the physicochemical properties of *Arabidopsis* AtXDH1 and AtXDH2

might be nearly identical because of their high degree of similarity (94%). For this study, over 80 clones were sequenced representing 20 taxa. Taxa that had more than one copy had 91%–99.8% similarity among sequences, such as *Coriaria sarmentosa* G. Forst. (sp.) of the Cucurbitaceae having a 95% similarity among cloned sequences. Only *Tacca* J. R. Forst. & G. Forst. and *Polygala* L. had similarities of 71% and 58%, respectively, among the cloned sequences. In both taxa, once the highly divergent sequence was removed, homology among the remaining sequences was 98% and 99%, respectively.

COMPARING METHODS OF ANALYSIS

Sequence variability

Approximately 1265 bp were sequenced, resulting in 1557 aligned characters due to the insertion of gaps. Sequences were aligned manually using Sequencher 4.7 (Gene Codes Corporation, Ann Arbor, Michigan, U.S.A). Eleven indels ranging from 3 to 66 bp in length were inserted in the alignment. Of the aligned characters, 1187 (76%) were variable, 1068 (69%) were potentially parsimony-informative, and approximately 180 (12%) were missing. The transition:transversion ratio in *Xdh* was 1.10, indicating that a high level of saturation was not reached (ratio of 0.4 and below is an indication of highly saturated sequences, according to Holmquist [1983]).

Phylogenetic results

Parsimony trees containing 253 taxa produced 21,585 trees of 31,337 steps in length, with a consistency index (CI) = 0.11 and a retention index (RI) = 0.50 (940 hours used). Homoplasy levels are comparable with those from Soltis et al.'s (2000) three-gene data set (CI = 0.12, 567 taxa) and Hilu et al.'s (2003) *matK* gene data set (CI = 0.14, 374 taxa).

The discussion is based on the likelihood tree because of its better resolution and support, and the results from the MP topology will be contrasted only when relevant. Bootstrap support of 50%–74% is considered low, 75%–84% moderate, and greater than 85% high (Chase et al., 2000).

The likelihood tree (Figs. 1–8) has a total of 190 of the 253 nodes (71%) that received bootstrap support of 50% or greater, and support levels averaged 71%. The likelihood tree depicts the angiosperms as monophyletic (80%) with *Ceratophyllum* (Ceratophyllaceae) as a sister to the rest of the flowering plants, followed successively by *Amborella* (Amborellaceae), a clade incorporating *Brasenia* Schreb., *Nuphar* Sm., and *Nymphaea* L. (Nymphaeaceae) and an *Austrobailey*a C. T. White–*Kadsura* Juss.–*Schisandra* Michx. (Austrobaileyales) clade as sister to the remaining angiosperms. *Acorus* L. (73%) is sister to the remaining monocots (74%). A weakly supported magnoliid clade (42%) consists of Piperales and Canellales (56%) and Laurales and Magnoliales (90%). *Acorus* plus the remaining monocots, magnoliids, and Chloranthaceae sequentially diverge after the Austrobaileyales. Eudicots include a basal grade of Ranunculales and Proteaceae, Sabiaceae, Trochodendraceae, Buxaceae, Gunneraceae, and Dilleniaceae and Santalaceae, which form a grade to the remaining eudicots. The grade of taxa containing Ranunculales and Proteaceae, Trochodendraceae, and Gunneraceae to the eudicots received 72%, 71%, and 72% support, respectively. The remaining eudicots are split into two clades. The first clade consists of the Ericales, Cornales, and euasterids I and II (lamids and campanulids), i.e., the asterid clade (Asteridae, Fig. 5). The second clade consists of the following orders: Saxifragales, Myrtales–Caryophyllales–Cucurbitales, Crossosomatales, Geraniales, Rosales–Fabales–Fagales, Celastrales, Malpighiales, Brassicales–Malvales, Oxalidales, and Sapindales (Figs. 6–8).

DISCUSSION

EARLY-DIVERGING ANGIOSPERMS

Early-diverging angiosperms have been the subject of intensive molecular studies (Chase et al., 1993; Soltis et al., 1997, 1999, 2000, 2005; Hoot et al., 1999; Mathews & Donoghue, 1999, 2000; Parkinson et al., 1999; Qiu et al., 1999, 2000, 2005, 2006; Barkman et al., 2000; Graham & Olmstead, 2000; Savolainen et al., 2000; Zanis et al., 2002, 2003; Borsch et al., 2003; Goremykin et al., 2003; Hilu et al., 2003; Aoki et al., 2004; Stefanović et al., 2004; Löhne & Borsch, 2005). Recent studies have found the earliest diverging lineages of the angiosperms to be members of the Amborellaceae and Nymphaeaceae, either as a clade or grade, followed by the Austrobaileyales (Savolainen et al., 2000, *atpB*; Soltis et al., 2000, 2005; Hilu et al., 2003; Qiu et al., 2006). The *Xdh* gene had a topology supported by 81% bootstrap values for the monophyly of the angiosperms consisting of *Ceratophyllum*, followed by *Amborella*, Nymphaeaceae, and Austrobaileyales (Fig 1). The position of *Ceratophyllum* has varied widely in previous studies: sister to either all angiosperms (Chase et al., 1993; Savolainen et al., 2000 [*rbcL*, *atpB/rbcL*]), sister to monocots (Zanis et al., 2002, 2003; Qiu et al., 2005; Soltis et al., 2005), sister to Chloranthaceae (Qiu et al., 2006), sister to eudicots

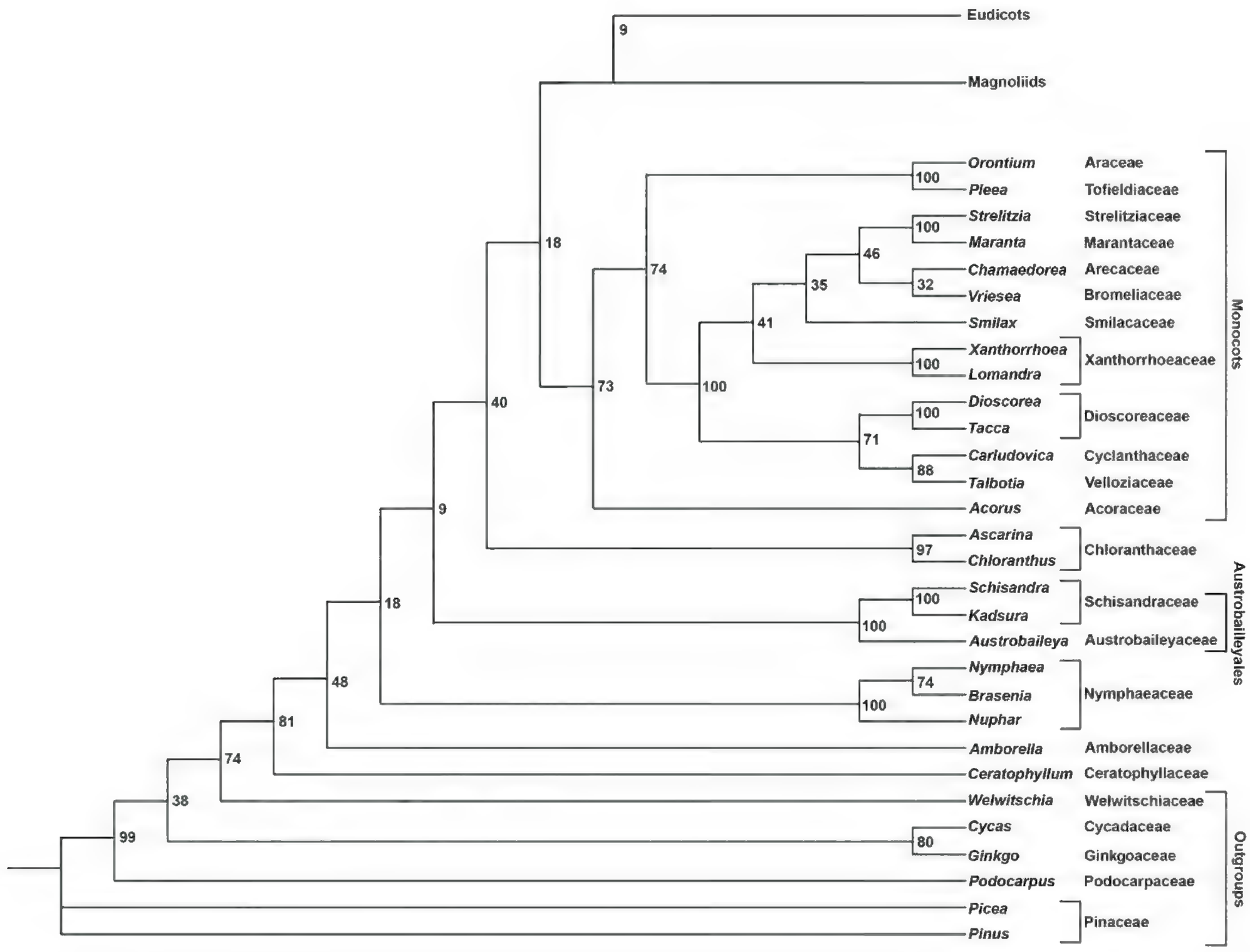

Figure 1. Bootstrap consensus tree of likelihood analyses among basal angiosperm lineages. The numbers above the branches are likelihood bootstrap values.

(Soltis et al., 2000; Hilu et al., 2003; Qiu et al., 2005, 2006), or sister to *Acorus*, which is sister to the remaining monocots (Savolainen et al., 2000 [*atpB*]). Only one sample of *Ceratophyllum* was used in our study, which may influence the placement of this taxon in this analysis. The placement of *Amborella* and Nymphaeales followed by Austrobaileyales is in agreement with most cited studies. In one of the most intensive studies of the earliest diverging lineages, using three mitochondrial, one nuclear, and four chloroplast genes (Qiu et al., 2006), different inferences among gene data sets were shown. Comparison of the mitochondrial and chloroplast data sets found that mitochondrial genes supported *Amborella*–Nymphaeales, while chloroplast genes supported *Amborella* as sister to remaining angiosperms. Depending on the data set, *Ceratophyllum* was either sister to Chloranthaceae, with a likelihood bootstrap value of 26%, or sister to eudicots, with a likelihood bootstrap value ranging from 38% to 51%. Only one nuclear gene was examined in the study from Qiu et al. (2006), and comparisons were not made with the mitochondrial or chloroplast topologies. Previous studies, along with the present research, suggest that resolving these relationships will require more research.

CHLORANTHACEAE

The position of Chloranthaceae has varied in previous studies, from sister to all of the euangiosperms (Qiu et al., 2006; Cantino et al., 2007), sister to *Ceratophyllum* (Qiu et al., 2006), sister to monocots (Hilu et al., 2003), sister to magnoliids and eudicots (Zanis et al., 2002, 2003; Soltis et al., 2005), sister to magnoliids (Savolainen et al., 2000 [*atpB* data set]), or sister to monocots and magnoliids (Savolainen et al., 2000 [using the *rbcL* or *atpB/rbcL* data sets]; Soltis et al., 2000). Most of these placements have had very low to only moderate bootstrap support. This family exhibits numerous distinctive morphological characters and putative synapomorphies, and its fossil record can be traced back to the Early Cretaceous (Friis et al., 1986; Pedersen et al., 1991; Doyle et al., 2003). The *Xdh* likelihood tree found that Chloranthaceae, represented here by two genera, forms a strongly supported clade (97%) that is sister to all monocots, magnoliids, and eudicots (Fig. 1). The most parsimonious tree

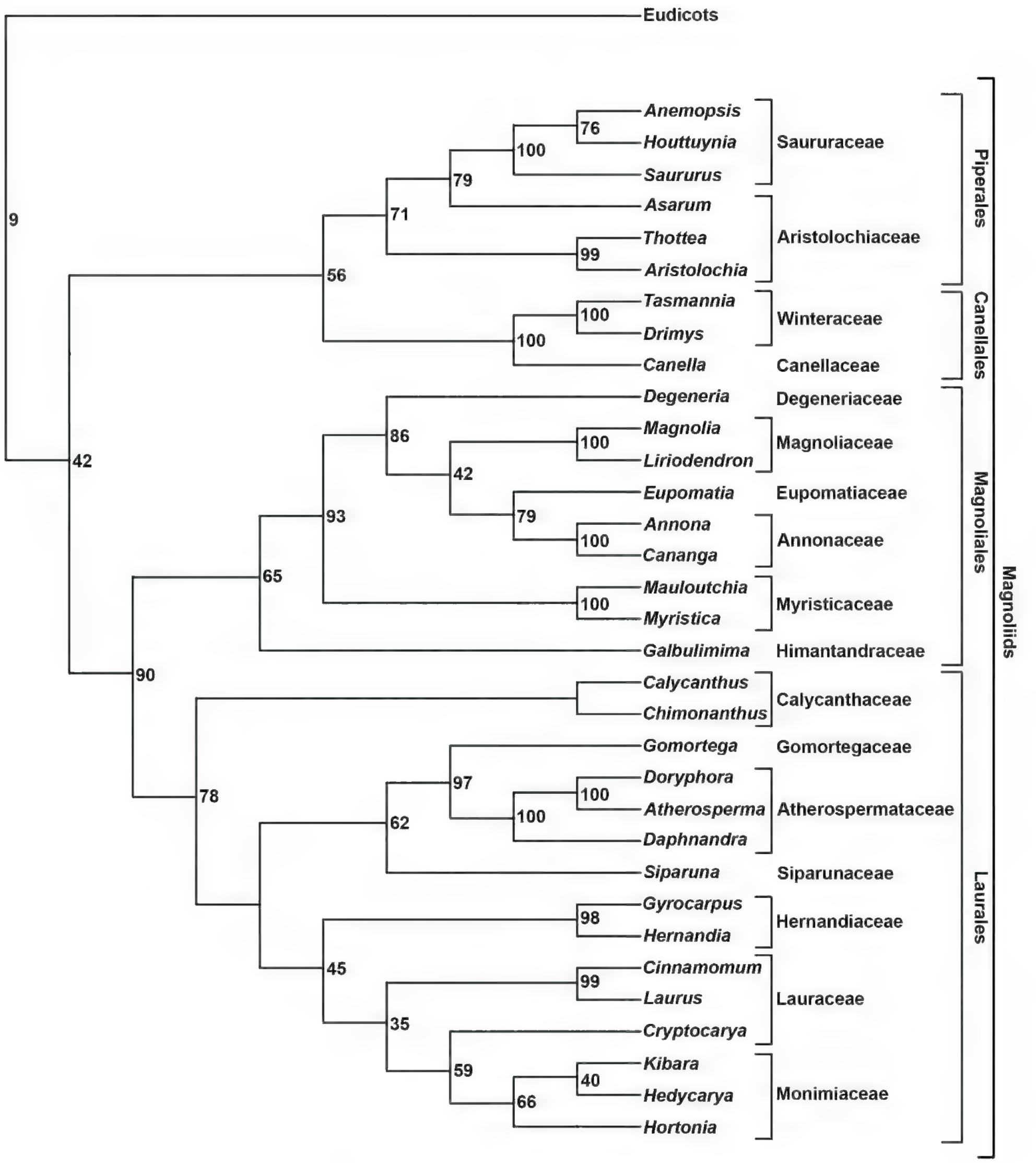

Figure 2. Bootstrap consensus tree of likelihood analyses among magnoliids. The numbers above the branches are likelihood bootstrap values.

(MPT) differs in that Chloranthaceae was sister to all eudicots.

ACORUS PLUS REMAINING MONOCOTS

The *Xdh* sequences provided moderate support (73%) for the monophyly of the monocots, with Alismatales (Araceae and Tofieldiaceae) followed by *Acorus* as sister to the remaining monocots (Fig. 1). This topology has been found in most single and multigene analyses (Chase et al., 2000, 2006; Savolainen et al., 2000 [*rbcL*, *atpB/rbcL*]; Soltis et al., 2000, 2005; Hilu et al., 2003). The monophyly of the Alismatales received high support (100%), along with the monophyly of the remaining monocots (100%). The internal structure of the monocots is represented by two clades. The first clade contains Dioscoreales (100%) and Pandanales (Cyclanthaceae and Velloziaceae, 88%) with 71% support. The second clade includes sister to Asparagales (Xanthorrhoeaceae, 100%), followed by Liliales (Smilacaceae), and two nested sister clades, one consisting of Poales (Bromeliaceae) and Arecales with weak support (32%) and the other of Zingiberales (Marantaceae and Strelitziaceae, 100%). These relationships are highly congruent with those suggested by Hilu et al. (2003).

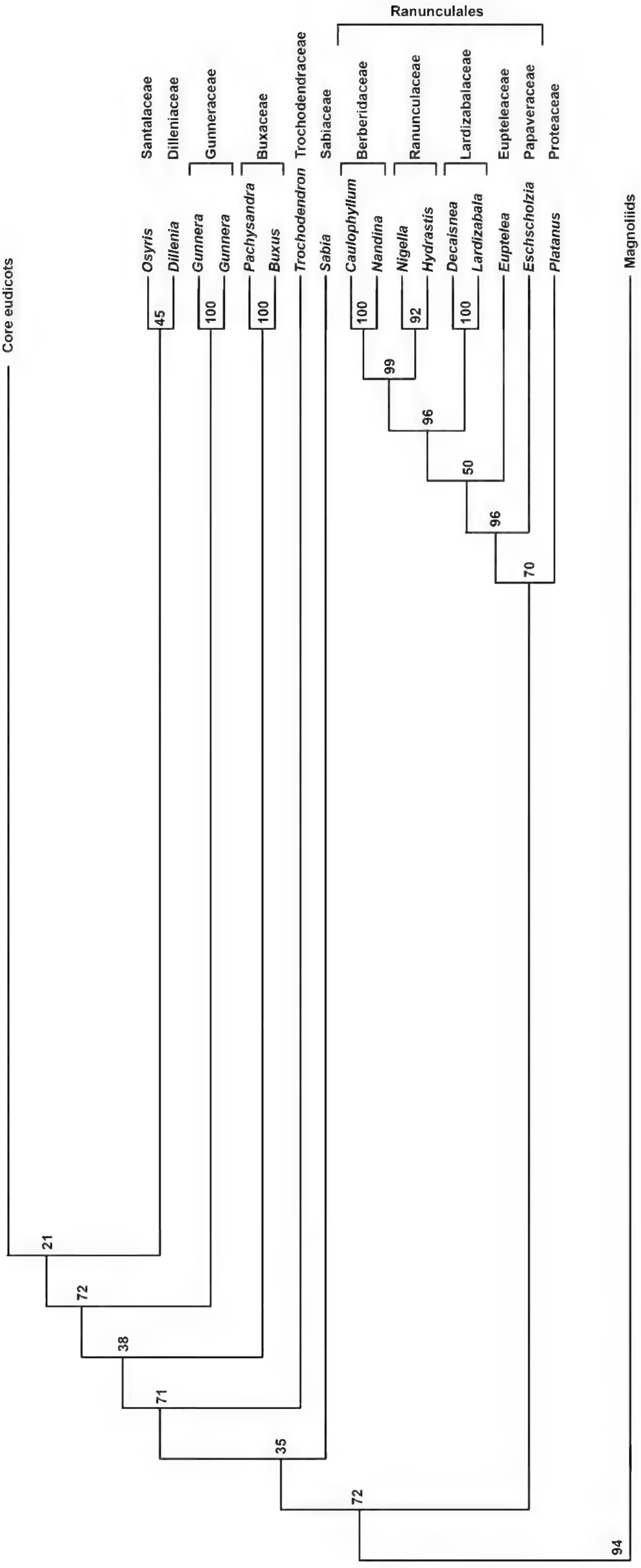

Figure 3. Bootstrap consensus tree of likelihood analyses among basal grade of eudicots. The numbers above the branches are likelihood bootstrap values.

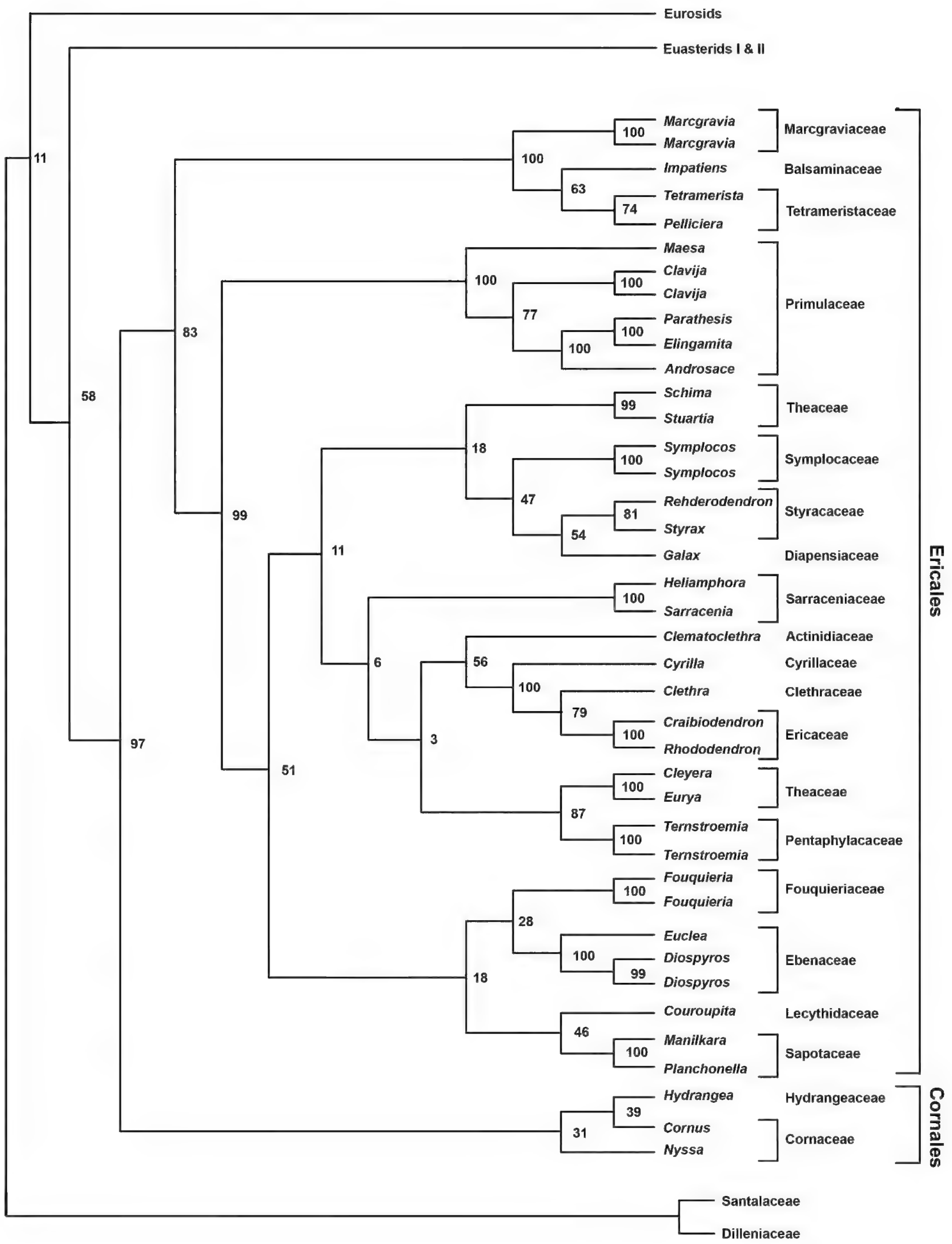

Figure 4. Bootstrap consensus tree of likelihood analyses among Ericales. The numbers above the branches are likelihood bootstrap values.

Our results are also consistent with those of Chase et al. (2000, 2006) based on seven genes, 18S rDNA, partial 26S, *rbcL*, *atpB*, *matK*, *ndhF*, and *atp1*. The exact positions of some orders are slightly different; for example, in Chase et al. (2006), Dioscoreales and Pandanales are sister to Liliales, while in trees based on *Xdh*, *Smilax* L. (Liliales) is sister to the Poales and Arecales. The monocots are sister to the magnoliids (a clade consisting of Piperales, Canellales, Laurales, and Magnoliales).

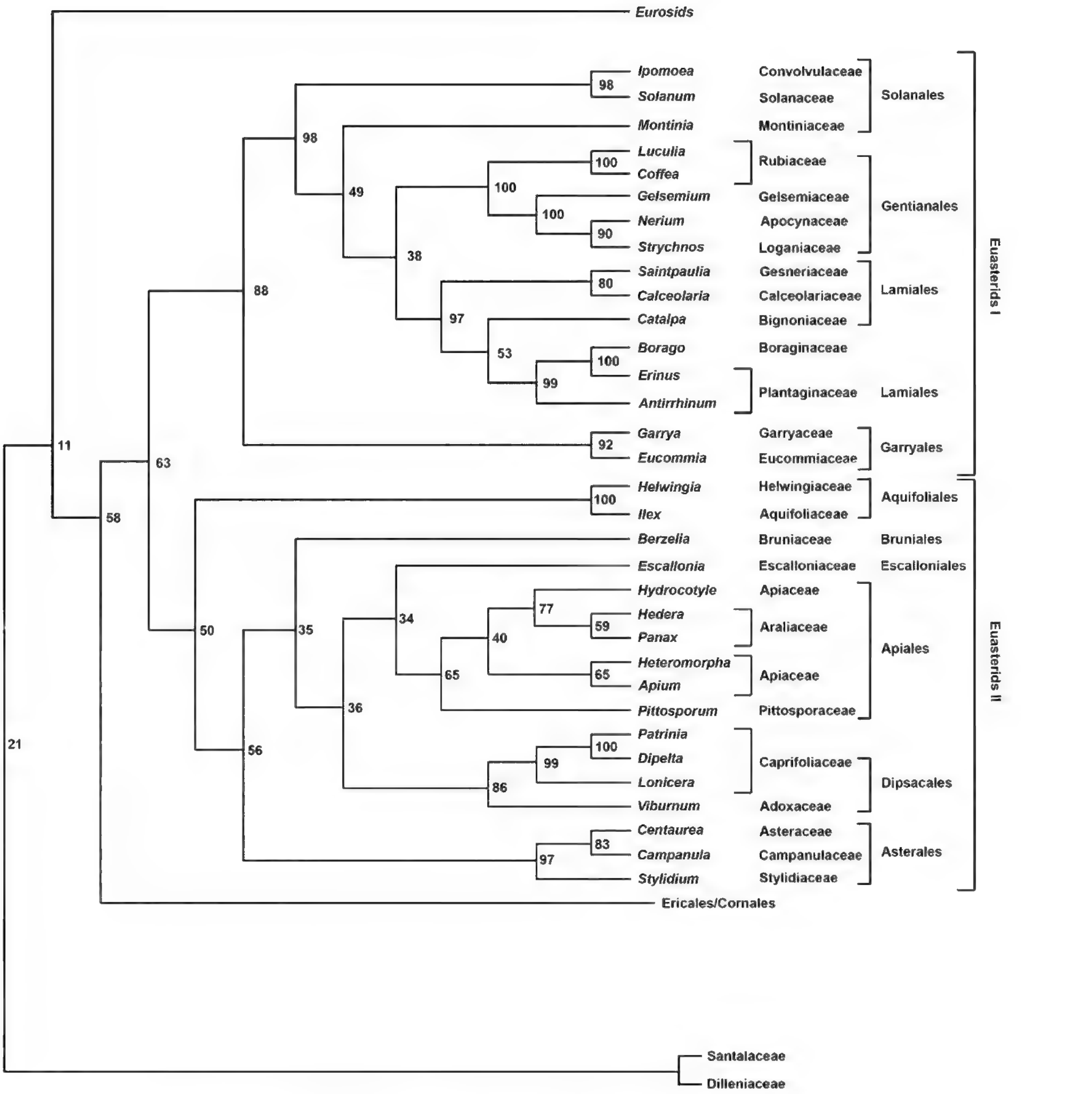

Figure 5. Bootstrap consensus tree of likelihood analyses among euasterid I and II. The numbers above the branches are likelihood bootstrap values.

MAGNOLIIDS

Recent studies provide strong evidence for a clade including only Piperales, Canellales, Laurales, and Magnoliales (generally referred to as the magnoliids or eumagnoliids). The *Xdh* topology is in agreement with this circumscription, although some earlier phylogenetic studies (Chase et al., 1993; Savolainen et al., 2000 [*rbcL*, *atpB/rbcL*]; Soltis et al., 2000) did not recognize the monophyly of the magnoliids or the relationships among the four orders (Fig. 2). Qiu et al. (1999, 2000, 2006) identified the sister relationships between Magnoliales and Laurales and between Canellales and Piperales, as well as the monophyly of all of the magnoliids. Hilu et al. (2003) also recovered the monophyly of the magnoliids, with Magnoliales–Laurales and Piperales–Canellales as sister groups, but with low levels of support. The *Xdh* likelihood tree has high levels of support for the Magnoliales–Laurales sister-group relationship (90%), whereas the Canellales–Piperales sister-group relationship received lower support (56%). These sister-group relationships have been found in several other analyses (Mathews & Donoghue, 1999, 2000; Qiu et al., 1999, 2000, 2005, 2006; Barkman et al., 2000; Graham & Olmstead, 2000; Zanis et al., 2002, 2003; Borsch et al., 2003, 2005; Hilu et al., 2003; Löhne & Borsch, 2005; Soltis et al., 2005; Graham et al., 2006).

In the clade consisting of the Canellales, Winteraceae formed a strongly supported clade (100%) with *Canella* P. Browne (100%). The Piperales (71%) contained members of Saururaceae and Aristolochiaceae. The position of *Asarum* L. (Aristolochiaceae) as sister to the Saururaceae (100%)

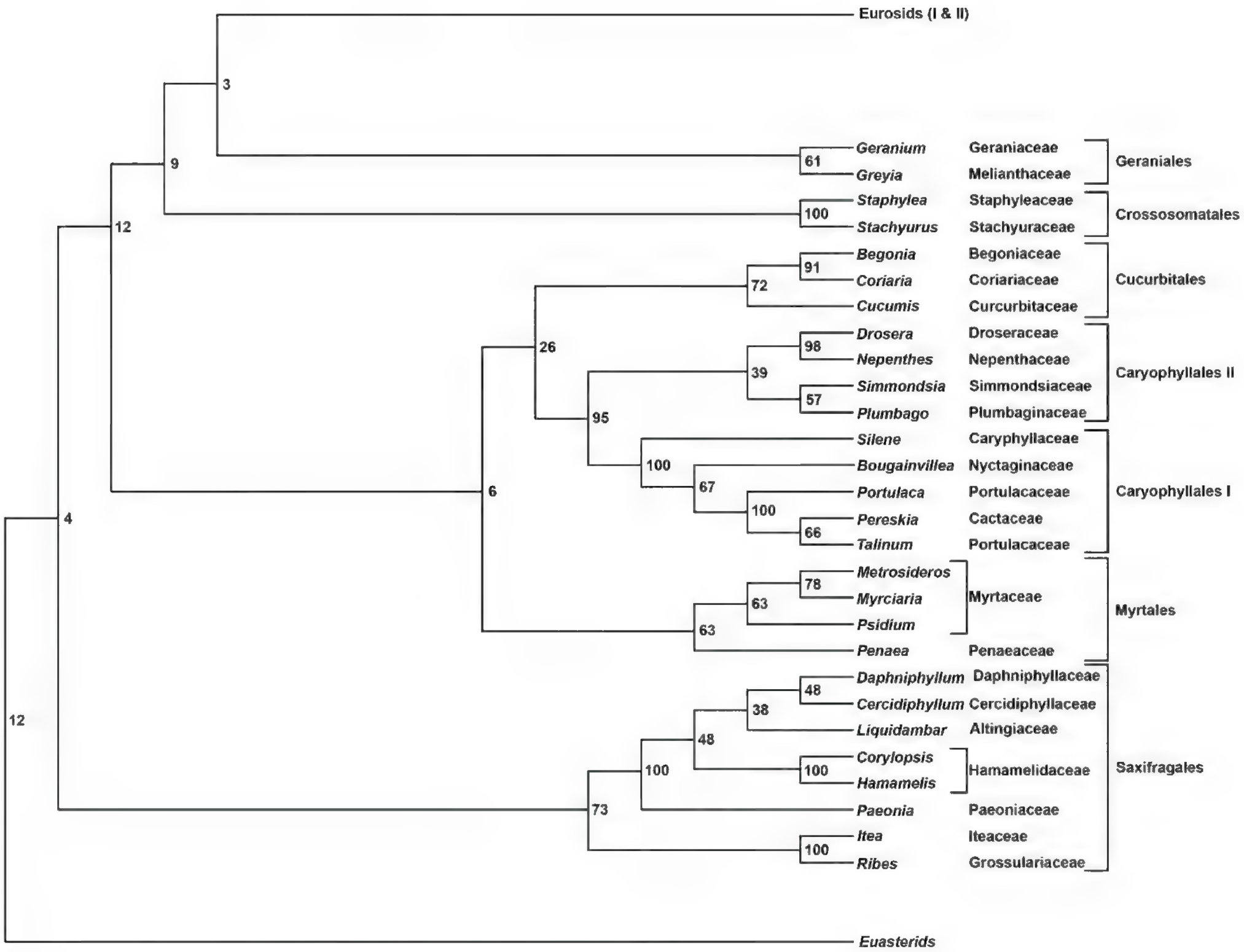

Figure 6. Bootstrap consensus tree of likelihood analyses among the core eudicots. The numbers above the branches are likelihood bootstrap values.

was different than that in most other analyses. However, this position for *Asarum* was also found in the study by Hilu et al. (2003), but, with increased taxon sampling, Qiu et al. (2006) showed that *Asarum* regrouped with members of Aristolochiaceae. Morphological characters clearly place *Asarum* in Aristolochiaceae, with aristolochic acids, sepals connate, filaments slightly adnate to the style, ovary inferior, and ovules numerous among their common traits (Judd et al., 2007). Limited taxon sampling may be influencing the placement of *Asarum* in this analysis. Increasing the sampling of Aristolochiaceae, Piperaceae, and Saururaceae may result in different inferences.

The Magnoliales formed a weakly supported clade (65%), and all families with more than one genus are monophyletic. The Annonaceae, Degeneriaceae, Eupomatiaceae, Himantandraceae, Magnoliaceae, and Myristicaceae have occupied various positions in most major analyses (Qiu et al., 1999, 2000, 2005, 2006; Zanis et al., 2002; Hilu et al., 2003). *Xdh* sequences provide evidence that Himantandraceae is sister to the remaining members of the order, followed by Myristicaceae, Degeneriaceae, and Magnoliaceae, which are sister to the clade Eupomatiaceae and Annonaceae.

The Laurales formed a moderately supported clade (78%) with all multitaxa families remaining monophyletic, except for the Lauraceae. The nonmonophyly of Lauraceae was also found by Qiu et al. (2006) using several taxa, but Chanderbali et al. (2001) examined additional taxa and found a clade containing *Cryptocarya* R. Br. to be basal in the Lauraceae. The placements of Atherospermataceae, Calycanthaceae, Gomortegaceae, Hernandiaceae, Lauraceae, Monimiaceae, and Siparunaceae of the Laurales have varied in most major analyses, and their relationships will remain unresolved until more examinations are completed (Qiu et al., 1999, 2000, 2005, 2006; Chanderbali et al., 2001; Zanis et al., 2002; Hilu et al., 2003).

Although the magnoliid grouping has been found in many other molecular analyses, sound morphological or phytochemical characters to define the groups are lacking (Doyle & Endress, 2000). Soltis et al. (2005) cited some chemical compounds such as neolignan and P-type sieve-tube plastids for most of the families, and Stevens (2001, onward) mentions

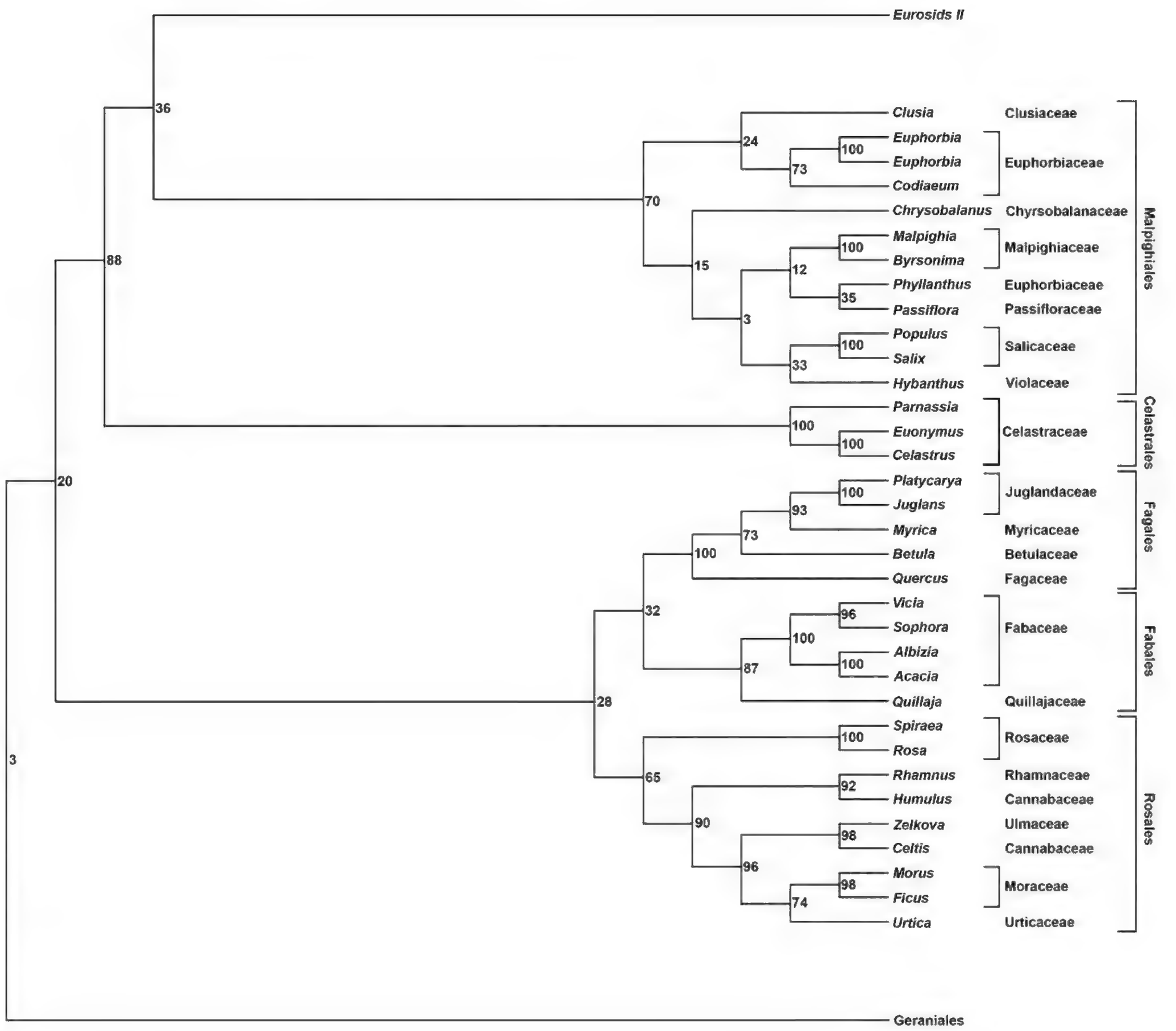

Figure 7. Bootstrap consensus tree of likelihood analyses among eurosid I. The numbers above the branches are likelihood bootstrap values.

chemical compounds such as neolignan and embryological features, but there are no unambiguous synapomorphies for this clade. The *Xdh* analysis has provided additional evidence for the monophyly and relationships among the magnoliids.

EUDICOTS

Early-diverging eudicots

The early-diverging eudicot taxa—Ranunculales, Proteaceae, Sabiaceae, Trochodendraceae, Buxaceae, and Gunneraceae—have been consistently recovered together as mainly a grade in a number of analyses (Chase et al., 1993; Hoot et al., 1999; Savolainen et al., 2000 [*atpB*, *atpB/rbcL*]; Soltis et al., 2000, 2003, 2005; Hilu et al., 2003); however, the placement of these taxa has varied. *Xdh* data are mostly in agreement with results obtained from previous studies, although the *Xdh* trees are most closely similar to those of Soltis et al. (2005). Ranunculales and Proteaceae (72%), Sabiaceae (35%), Trochodendraceae (71%), Buxaceae (38%), and Gunneraceae (72%) form a grade in the *Xdh* likelihood tree (Fig. 3). Ranunculales and Proteaceae were sister, forming a clade with low support (70%). This clade was not found by Soltis et al. (2005) and could be a result of the *Xdh* analysis having low sampling of Proteaceae, including only a single representative, *Platanus* L.

Eschscholzia Cham. (Papaveraceae, 96%) and *Euptelea* Siebold. & Zucc. (Eupteleaceae, 50%) form a grade to the remaining Ranunculales, and the Ranunculales are sister to the remaining eudicots, consistent with other analyses (Chase et al., 1993; Soltis et al., 1997, 2000, 2003, 2005; Hoot et al., 1999). Lardizabalaceae is a strongly supported clade (100%) sister to the Berberidaceae and Ranunculaceae clade (99%). Berberidaceae and Ranunculaceae are strongly supported as monophyletic groups (100% and 92%, respectively). The placement of Dilleniaceae and Santalaceae, forming a clade that is sister to the asterids and rosids, also occurs in the MPTs. The

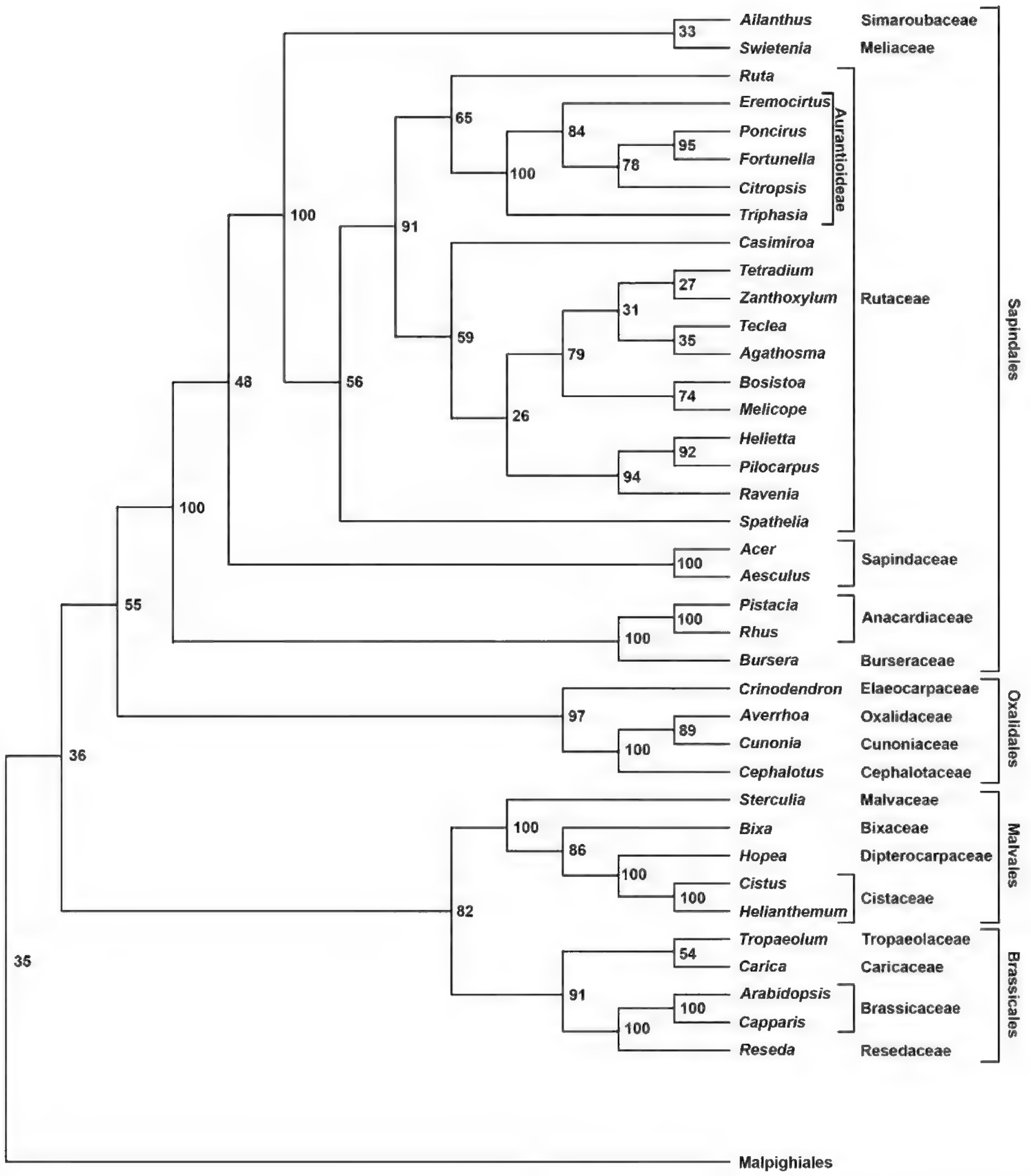

Figure 8. Bootstrap consensus tree of likelihood analyses among eurosid II. The numbers above the branches are likelihood bootstrap values.

sister-group relationship of *Dillenia* L. (Dilleniaceae) and *Osyris* L. (Santalaceae) (45%) has been found in other studies (Soltis et al., 2000, 2005), but the relationships of *Dillenia* are uncertain, with many different hypothesized relationships (compare Savolainen et al., 2000; Soltis et al., 2000, 2003, 2005; Hilu et al., 2003). The relationships of the Santalaceae are equally uncertain (compare Savolainen et al., 2000; Soltis et al., 2000, 2003; Hilu et al., 2003).

EUDICOTS CLADE I

Asterids

The asterid clade, sensu Olmstead et al. (1992, 1993) and Judd and Olmstead (2004), is monophyletic (58% bootstrap support) in the *Xdh* tree (Fig. 5) and consists of the four major lineages Cornales, Ericales, and euasterid I and II. In the *Xdh* tree the Ericales–Cornales clade is strongly supported (97%, Fig. 4). The euasterids I and II (Fig. 5) formed poorly supported sister clades (63%). Although support values are difficult to compare, this topology is mostly in agreement with other multigene studies (Savolainen et al., 2000; Soltis et al., 2000).

Ericales–Cornales

The monophyly of Ericales received moderate support (83%) in the *Xdh* analysis, while the monophyly of the Cornales lacks bootstrap support (31%, Fig. 4). The resolution and support for the Ericales clade were similar to those in other analyses, including Bremer et al.'s (2002) six-gene plastid

analysis, Anderberg et al.'s (2002) five-gene analysis from plastid and mitochondrial regions, and Schönenberger et al.'s (2005) 11-gene analysis from nuclear, mitochondrial, and chloroplast regions. Within the Ericales, the *Xdh* analysis recovered four major clades, with multiple-sampled families monophyletic: (1) The first clade (100%) contains Tetrameristaceae and Balsaminaceae sister to Marcgraviaceae. (2) The second clade (100%) consists of the Primulaceae. (3) The third clade is tentative due to low support (18%) and has Sapotaceae sister to Lecythidaceae, which is sister to a Fouquieriaceae–Ebenaceae clade. The lack of samples from Polemoniaceae, which typically has been found to be sister to Fouquieriaceae (Savolainen et al., 2000 [*atpB*, *atpB/rbcL*]; Anderberg et al., 2002; Bremer et al., 2002; Soltis et al., 2005), is problematic in this analysis and may explain the low support for this group. (4) The fourth clade, also with low support, has two major lineages. The first contains Theaceae, sister to a clade containing Symplocaceae, and Styracaceae, sister to Diapensiaceae. The second is weakly supported and contains Sarraceniaceae sister to a clade consisting of Pentaphylacaceae, Theaceae, Actinidiaceae, Cyrillaceae, Clethraceae, and Ericaceae. Other multigene studies have found Sarraceniaceae sister to Actinidiaceae, together sister to Clethraceae, Cyrillaceae, and Ericaceae (Anderberg et al., 2002; Bremer et al., 2002). *Xdh* provides a similar inference although with varying support values. Using morphological data, Judd and Kron (1993) found the same topology for relationships with the core Ericales as found in the *Xdh* analysis.

Euasterid I (Lamids)

The euasterid I clade (consisting of Boraginaceae, Garryales, Gentianales, Lamiales, and Solanales) has strong bootstrap support (88%, Fig. 5) in the *Xdh* analysis, whereas most other studies have shown low to moderate support levels for it (Savolainen et al., 2000 [*atpB*, *rbcL*, *atpB/rbcL*]; Soltis et al., 2000, 2003; Albach et al., 2001; Bremer et al., 2002; Hilu et al., 2003). The first branching lineage is the Garryales and this is in agreement with previous studies (Savolainen et al., 2000 [*atpB*, *rbcL/atpB*]; Soltis et al., 2000, 2003; Albach et al., 2001). There is strong support (98%) for the relationships found among Boraginaceae, Gentianales, Solanales, and Lamiales. Monophyly of the orders Gentianales (100%) and Lamiales (including *Borago* L., 97%) also obtained strong support. This level of support has been found in most other studies (Savolainen et al., 2000 [*atpB*, *rbcL*, *atpB/rbcL*]; Soltis et al., 2000; Albach et al., 2001; Bremer et al., 2002; Hilu et al., 2003). The Gentianales has Rubiaceae as sister to members of the Loganiaceae, Apocynaceae, and Gelsemiaceae. The Lamiales contains representative taxa from Bignoniaceae, Boraginaceae, Calceolariaceae, Gesneriaceae, and Plantaginaceae. In a clade representing members from the Plantaginaceae and Boraginaceae, *Erinus* L. (Plantaginaceae) is sister to *Borago* (Boraginaceae).

Euasterid II (Campanulids)

The euasterid II clade is weakly supported (50%) and consists of Aquifoliales, Asterales, Bruniaceae, Dipsacales, Escalloniaceae, and Apiales (Fig. 5). Aquifoliales as the first branching lineage is in agreement with most previous studies (Chase et al., 1993; Savolainen et al., 2000 [*atpB*, *atpB/rbcL*]; Soltis et al., 2000, 2003, 2005; Albach et al., 2001; Bremer et al., 2002) excluding those performed by *matK* analysis (Hilu et al., 2003), in which Aquifoliales aligned with the euasterid I (Campanulids) clade. Most analyses agree that euasterid II is composed of four major orders (Aquifoliales, Apicales, Dipsacales, and Asterales); however, the sister-group relationships differ among analyses. The most recent multigene analysis of Burleigh et al. (2009) is in agreement with this study in having Aquifoliales basal and sister to Asterales, together sister to Apiales and Dipsacales. The Apiales consists of approximately 10 families, the Asterales consists of 12 families, and the Aquifoliales contains approximately five families. The *Xdh* study sampled eight families of the possible 27 from these three orders; additional samples from the remaining families will most likely increase the internal resolution and provide additional support within euasterid II.

EUDICOTS CLADE II

The eudicots clade II likelihood tree contains the following taxa: Saxifragales, Myrtales–Caryophyllales–Cucurbitales, Crossosomatales, Geraniales, eurosid I (without Cucurbitales and Oxalidales), and eurosid II, with Oxalidales recovered in the *Xdh* tree. The MPT found Saxifragales, Crossosomatales, Geraniales, eurosid I (with Cucurbitales, Fabales, Fagales, Myrtales, and Rosales), and eurosid II (with Brassicales, Celastrales, Malphigiales, Malvales, Oxalidales, and Sapindales) as groups.

Saxifragales

The *Xdh* analysis has low support (73%) for the monophyly of Saxifragales (Fig. 6). Three well-supported clades are resolved within this order. The

first clade includes Iteaceae sister to Grossulariaceae (100%). A similar topology was recovered by Fishbein et al. (2001), Hilu et al. (2003), and Soltis et al. (2005). The second clade consists of a monophyletic Hamamelidaceae (100%), which has been documented in many other studies (Savolainen et al., 2000 [*atpB/rbcL*]; Soltis et al., 2000, 2003, 2005; Fishbein et al., 2001; Hilu et al., 2003). A third clade including Altingiaceae, Cercidiphyllaceae, Daphniphyllaceae, Hamamelidaceae, and Paeoniaceae is well supported (100%). Several major families are missing, such as Saxifragaceae and Crassulaceae. Therefore, it is still premature to comment on the position of the taxa in the third clade. Soltis et al. (2007a) also were unable to recover stable relationships among the woody Saxifragales. The Saxifragales circumscription contains a wide range of morphological diversity that departs from traditional classification. The nonmolecular synapomorphies have not yet been found and more research is needed for clarification.

Myrtales–Caryophyllales–Cucurbitales

The analyses recover a weakly supported (6%) clade consisting of Myrtales, Caryophyllales, and Cucurbitales (Fig. 6). This inference may be misleading or incorrect due to the weak support because no other analyses have grouped these orders together. In contrast, the MPT is like previous MP analyses, revealing Caryophyllales as sister to the eudicots, and Cucurbitales as sister to Fagales. In a recent analysis, the Caryophyllales clade has been variously placed at the base of the asterids (Hilu et al., 2003; Soltis et al., 2005), sister to the Saxifragales (Soltis et al., 2003), sister to the eudicots (Savolainen et al., 2000 [*rbcL, atpB/rbcL*]; Soltis et al., 2000), or sister to the asterids and rosids (Savolainen et al., 2000 [*atpB*]). Cucurbitales are typically found associated with a nitrogen-fixing clade, which includes Rosales, Fagales, Fabales, and Cucurbitales (Soltis et al., 1995, 1997, 2000, 2003, 2005; Savolainen et al., 2000 [*atpB, rbcL, atpB/rbcL*]; Hilu et al., 2003). The position of the Myrtales is usually nested within, or sister to, a clade consisting of Malvales, Brassicales, and Sapindales (Soltis et al., 1997, 2000, 2005; Savolainen et al., 2000 [*atpB, rbcL, atpB/rbcL*]; Hilu et al., 2003). The Myrtales clade in the *Xdh* data set has two members with partial sequences that may be creating errors in their placement. In all three orders, the families are underrepresented; we sampled only two of the approximately 13 families of the Myrtales, seven of the approximately 29 families of the Caryophyllales, and three of the approximately seven families of the Cucurbitales. The differences between the likelihood and MP analyses need to be further explored using all genes in independent and combined analyses. Both factors, partial sequences and underrepresentation of families, are most likely contributing to this unusual placement of the Myrtales.

Two families were sampled for the Myrtales (63%), Myrtaceae and Penaeaceae. *Metrosideros* Banks ex Gaertn., *Myrciaria* O. Berg, and *Psidium* L. formed a monophyletic Myrtaceae with low support (63%, Fig. 6). This order has had various circumscriptions in the past, consisting of a number of families, and it would be premature to speculate on its composition, as well as relationships within the order and with other rosids. The monophyly of this order is in agreement with the results of Conti et al. (1996) based only on *rbcL*, Savolainen et al. (2000) based on *atpB/rbcL*, Soltis et al. (2000, 2005) based on *rbcL/atpB*/18S, and Hilu et al. (2003) based on *matK*.

The *Xdh* sequence data strongly support the circumscription of the Caryophyllales (95%, Fig. 6). The monophyly of this order has been indicated in previous molecular studies (Savolainen et al., 2000 [*atpB, rbcL, atpB/rbcL*]; Soltis et al., 2000, 2003, 2005; Cuénoud et al., 2002; Hilu et al., 2003). Two clades within Caryophyllales are recognized with *Xdh* data. Caryophyllales I (100%) includes Caryophyllaceae and Nyctaginaceae, followed by a well-supported Portulacaceae grade, with Cactaceae nested within (100%). Caryophyllales II (39%) contains a clade of the carnivorous families Droseraceae and Nepenthaceae (98%) sister to a clade of Plumbaginaceae and Simmondsiaceae (57%). The position of the Simmondsiaceae has varied, being included in the Caryophyllales II clade in some analyses (Savolainen et al., 2000 [*rbcL/atpB*]), while, in others, it has been included in the Caryophyllales I clade (Soltis et al., 2000, 2005; Cuénoud et al., 2002; Hilu et al., 2003). One of the most comprehensive studies of the Caryophyllales, by Cuénoud et al. (2002), indicates that the position of *Simmondsia* Nutt. lacks strong support, demonstrating that additional work is needed. Our results show Simmondsiaceae as part of the Caryophyllales II clade with strong support. Members of Caryophyllales have some non-DNA features supporting its basic circumscription, but many gaps still remain to be filled (for characters, see Nandi et al., 1998; Stevens, 2001, onwards).

The Curcurbitales were defined by the Angiosperm Phylogeny Group (1998) and Angiosperm Phylogeny Group II (2003) as containing the following seven families: Anisophylleaceae, Begoniaceae, Coriariaceae, Corynocarpaceae, Cucurbitaceae, Datiscaceae, and Tetramelaceae. Begoniaceae, Coriariaceae, and

Cucurbitaceae were included in this analysis (Fig. 6), which found the Curcurbitales to be monophyletic, although this was only weakly supported (72%). Other gene studies have also found the Curcurbitales to be monophyletic (Savolainen et al., 2000 [*atpB*, *rbcL*, *atpB/rbcL*]; Soltis et al., 2000, 2003, 2005; Hilu et al., 2003; Zhang et al., 2006). Morphological and phytochemical synapomorphies for the Curcurbitales are still unclear; even the most recent study by Zhang et al. (2006), using 13 molecular markers and morphological characters, could not identify a synapomorphy for the order.

Crossosomatales

The Crossosomatales clade, here consisting of Staphyleaceae and Stachyuraceae, is well supported (100%, Fig. 6). Both the *rbcL/atpB* analysis (Savolainen et al., 2000) and the analysis of 18S, *rbcL*, and *atpB* (Soltis et al., 2000) contained a well-supported Crossosomatales clade. Stachyuraceae has previously been placed in the Violales, whereas Staphyleaceae has been placed in the Sapindales (Cronquist, 1981). Thus, another group of families previously placed in distantly related orders come together in a well-supported clade. Matthews and Endress (2005) investigated the floral characters and revealed potential new synapomorphies for a close relationship among the core member of Crossosomatales. Among the prominent floral features of Crossosomatales are solitary flowers, presence of a floral cup, imbricate sepals with outermost smaller than inner, pollen grains with horizontally extended endoapertures, shortly stalked gynoecium, postgenitally united carpel tips forming a compitum, stigmatic papillae 2-cellular or more, ovary locules tapering upward, long integuments forming zigzag micropyles, cell clusters with bundles of long yellow crystals, mucilage cells, seeds with smooth, sclerified testa and without differentiated tegmen. However, more molecular and morphological work is needed to resolve both the composition of this clade and its position within the rosids.

Geraniales

Two taxa of Geraniales were sampled for the *Xdh* analysis, *Geranium* L. (Geraniaceae) and *Greyia* Hook. & Harv. (Melianthaceae) (Fig. 6). These two families are held together in a weakly supported clade (61%). These families were previously placed (Cronquist, 1981; Takhtajan, 1997) in different orders, and no known morphological synapomorphies hold the present order together. Geraniales have been found in previous analyses (Savolainen et al., 2000 [*atpB/rbcL*]; Soltis et al., 2000) to be sister to the Crossosomatales. While there is no support for that sister relationship here, likelihood values at the base of the grades leading up to the eurosids are low (12% or less) and rearrangements may be expected with additional sampling of taxa and inclusion/combination with more data sets.

Eurosid I

In the analysis, the nitrogen-fixing clade (including Rosales, Fagales, Fabales, and Cucurbitales; Soltis et al., 1995), excluding Cucurbitales, is weakly supported at the base of the eurosid I grade (20%), followed by Celastrales (88%) and Malpighiales (< 50%) (Fig. 7). Three nitrogen-fixing subclades received low to strong support and have no support as a clade (28%): Fabales (87%), Fagales (100%), and Rosales (65%). These subclades have been placed together with the order Cucurbitales in other single and multigene analyses (Savolainen et al., 2000 [*atpB*, *rbcL*, *atpB/rbcL*]; Soltis et al., 2000, 2003; Hilu et al., 2003). The Fabales consist of well-supported Fabaceae (100%) and Quillajaceae. The order is sister to the Fagales, which contains a mostly well-supported clade of Fagaceae, Betulaceae, Myricaceae, and Juglandaceae. The Rosales are sister to Fabales and Fagales. This order consists of Rosaceae sister to the rest of the order followed by Rhamnaceae sister to *Humulus* L. (Cannabaceae), Ulmaceae sister to *Celtis* L. (Cannabaceae), and Moraceae sister to Urticaceae. The Cannabaceae are not monophyletic in the *Xdh* analysis because they group with members of the Rhamnaceae and Ulmaceae; however, the placement of *Humulus* is based on a partial sequence, which may have caused anomalies. Soltis et al. (2005) found similar clades including a nonmonophyletic Cannabaceae in the Rosaceae. As mentioned earlier, the MP analysis found eurosid I to consist of Cucurbitales, Fabales, Fagales, Myrtales, and Rosales.

The *Xdh* analysis supports (100%) the Celastrales clade (100%, Fig. 7). Most recent analyses support the order Celastrales, including various families placed next to the Malpighiales (Zhang & Simmons, 2006), Oxalidales (Hilu et al., 2003; Soltis et al., 2005), or the Oxalidales and Malpighiales (Soltis et al., 2000). The *Xdh* likelihood and MP analysis showed Celastrales in a well-supported clade sister to the Malpighiales and eurosid II clades (88%).

The Malpighiales form a weakly supported clade with three supported subclades: Salicaceae (100%), Malpighiaceae (100%), and part of the Euphorbiaceae (73%, Fig. 7). The Euphorbiaceae are not monophyletic, as also found in the analyses by Soltis

et al. (2000) and Tokuoka and Tobe (2006, four-marker study). In the *Xdh* analysis, *Codiaeum variegatum* (L.) Rumph. ex A. Juss., *Euphorbia neriifolia* L., and *E. pseudocactus* A. Berger of the Euphorbiaceae formed a clade, whereas *Phyllanthus flexuosus* Müll. Arg. (Euphorbiaceae—now Phyllanthaceae) formed a sister grouping with *Passiflora suberosa* L. (Passifloraceae). This study sampled the following seven families: Chrysobalanaceae, Clusiaceae, Euphorbiaceae, Malpighiaceae, Passifloraceae, Salicaceae, and Violaceae. Previous analyses have found that the Malpighiales encompass at least 28 morphologically diverse families (Soltis et al., 2000). The relationships among these families are poorly understood and further studies incorporating additional taxa and non-DNA characters are needed to resolve relationships within this heterogeneous order.

Eurosid II (including Oxalidales)

The *Xdh* analysis produced a very weakly supported (< 50%) eurosid II clade, including members of the Brassicales, Malvales, Oxalidales, and Sapindales (Fig. 8). Each of these orders was recovered in the *Xdh* tree with strong support: Brassicales (91%), Malvales (100%), Oxalidales (97%), and Sapindales (100%). The *Xdh* data provided support for a sister-group relationship of Brassicales and Malvales (82%). This relationship was also obtained in *rbcL/atpB* analyses but was not well supported (Savolainen et al., 2000), although in the *matK* analysis these orders were strongly supported (89%, Hilu et al., 2003). In a family-level analysis examining glucosinolate biosynthesis taxa using *rbcL* and 18S, this sister-group relationship of Brassicales and Malvales was also found (Rodman et al., 1998). A clade consisting of the Sapindales, Brassicales, and Malvales has been found in some other recent analyses, but typically this association has not been well supported (Savolainen et al., 2000 [*rbcL/atpB*]; Soltis et al., 2000, 2003; Hilu et al., 2003). In Soltis et al.'s (2000, 2003) three- and four-gene analyses, weak to moderate support was found for Sapindales being sister to Malvales, whereas no support was found for an association with Brassicales.

This study included representatives of Brassicaceae, Caricaceae, Resedaceae, and Tropaeolaceae of Brassicales (Fig. 8). *Arabidopsis* and *Capparis* L. (Brassicaceae) formed a well-supported clade (100%) sister to *Reseda* L. (Resedaceae, 100%), whereas *Tropaeolum* L. (Tropaeolaceae) and *Carica* L. (Caricaceae) formed a weakly supported clade (54%). Chemical compounds including glucosinolates from phenyalanine and/or tyrosine and myricetin and other methylated flavonols may provide synapomorphies for the order (Stevens, 2001, onward).

The Malvales comprised a well-supported (100%) order consisting of *Sterculia* L. (Malvaceae), *Bixa* L. (Bixaceae) (86%), *Hopea* Roxb. (Dipterocarpaceae) (100%), and *Cistus* L. and *Helianthemum* Mill. (Cistaceae) (100%, Fig. 8). It is premature to speculate on the familial relationships of Brassicales and Malvales using *Xdh* until additional taxa are sequenced.

The Sapindales are well supported (100%), with a number of well-supported subclades: (1) a strongly supported (100%) sister group of Anacardiaceae (100%) and Burseraceae; (2) a well-supported (100%) Sapindaceae with *Aesculus* L. and *Acer* L.; (3) a well-supported clade (100%) of Meliaceae, Simaroubaceae, and Rutaceae; and (4) a well-supported Rutaceae (91%), excluding *Spathelia* L. with the Aurantioideae (100%) and *Ruta* L. basal (65%) to the Aurantioideae, as has been previously found (Chase et al., 1999). Secondary compounds such as the ethereal oils and myricetin provide synapomorphies for the order (Morton, unpublished data).

Oxalidales has been positioned as sister to Celastrales and Huaceae (< 50%) (Savolainen et al., 2000 [*atpB/rbcL*]), Celastrales (Hilu et al., 2003; Soltis et al., 2005), and Malpighiales (Soltis et al., 2000 [< 50%], 2003 [< 50%]). The inclusion of the Oxalidales as sister to the Sapindales (56%) in the *Xdh* analysis is unique but not well supported (56%). The MP analysis, however, supports Celastrales and Malpighiales sister to Oxalidales, and this clade is sister to a Brassicales–Malvales–Sapindales clade. The phylogenetic analyses of Soltis et al. (2005) indicated that Oxalidales consists of six families: Brunelliaceae, Cephalotaceae, Connaraceae, Cunoniaceae, Elaeocarpaceae, and Oxalidaceae. This study included a well-supported clade of Cephalotaceae, Cunoniaceae, Elaeocarpaceae, and Oxalidaceae (97%). These families have all been previously placed in different orders, Cephalotaceae and Cunoniaceae in Rosales, Elaeocarpaceae in Malvales, and Oxalidaceae in Geraniales (Cronquist, 1981). Thus, here the Oxalidales comprise taxa that were once considered distantly related. Currently, no morphological synapomorphies are evident for eurosid II with or without Oxalidales (Judd et al., 1994, 2007).

The rosids remain inadequately understood as to supported phylogenetic positions, non-DNA synapomorphies for major clades, and patterns of character evolution. Most of these groups contain unexpected assemblages of taxa that previously have been placed

in distantly related orders. For these new groupings, many gaps in the non-DNA information render many features phylogenetically uninformative.

Conclusion

The *Xdh* tree of 247 genera and 1265 bp produced a likelihood tree that is robust and mostly congruent with other single or multigene studies (Savolainen et al., 2000; Soltis et al., 2000, 2003, 2005; Hilu et al., 2003; Qiu et al., 2006). The potential utility of *Xdh* in angiosperm phylogenetics can be gauged by the number of genera and base pairs used to produce this topology in comparison to other single and multigene analyses in which substantially more genera and base pairs were used to produce similar topologies and support levels. The *Xdh* topology demonstrated 71% of the nodes with bootstrap support greater than 50% in comparison to the *matK* topology (374 taxa), with 79%, and the reported 7%–24% for individual analyses of *rbcL*, *atpB* (357 taxa), and 18S (223 taxa) ribosomal DNA clades (Hilu et al., 2003: table 2, 1761). The number of nodes receiving greater than 50% support in the *Xdh* analysis was in the same range as was obtained for the *matK* and the combined analyses of three to four genes from two genomic regions. The number of parsimony-informative sites (1068–1069) was similar to the *matK* analysis (1083–1062).

Xdh analysis provides good support values for monophyly of the Caryophyllales, Ericales, and Cornales, euasterids I (lamids), Magnoliales and Laurales, Malvales, Rutaceae, Oxalidales, Brassicales, and Sapindales.

As stated earlier, paralogy exists for all genes. More than one copy was found in selected taxa; however, most had high sequence similarity, suggesting recent duplication. Among two taxa that had lower values, the highly divergent sequence was easily recognized. When the divergent sequence was removed, the remaining sequences had 98%–99% homology. Having more than one gene phylogeny to compare the angiosperm phylogeny is a good indicator of paralogy. The likelihood and MP topology of the *Xdh* gene are comparable to other individual gene data sets. The potential utility of this gene is quite promising at the ordinal, familial, and generic levels.

Although phylogenetic relationships of angiosperms have been explored using a number of gene sequences from the chloroplast and mitochondria, the nucleus remains poorly explored. Phylogenetics has achieved some understanding of angiosperm relationships, and the present study contributes to our knowledge. There are still parts of the tree that remain unresolved or unsupported by both molecular and morphological data. As Chase et al. (2006) discovered, adding mitochondrial and nuclear genes to four plastid genes produced a highly congruent result that is an improvement over their predecessors. We must continue to combine chloroplast, mitochondrial, nuclear, and morphological data to improve our understanding of angiosperm evolution.

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Appendix 1. Species sequenced for the present study, accession data, and GenBank accession numbers. See Materials and Methods. Order follows Stevens (2001 and onwards) and Group follows Burleigh et al. (2009).

Group	Order	Family	Species	Voucher/Source	Museum voucher/Number	GenBank number
Gymnosperms	Pinales	Podocarpaceae	*Podocarpus macrophyllus* (Thunb.) Sweet	X.16-33*A (FTBG)	*C. & A. Morton 2009–13* (CM)	EU264209
		Pinaceae	*Picea abies* (L.) H. Karst.	01/0181.A (PCPT)	*C. Morton 2010-1* (CM)	EU264211
			Pinus elliottii Engelm.	2002-0236*D (FTBG)	*C. Morton 2010-37* (CM)	EU264208
	Cycadales	Cycadaceae	*Cycas revoluta* Thunb.	99/0245 (PCPT)	*C. Morton 2010-2* (CM)	EU264212
	Ginkgoales	Ginkgoaceae	*Ginkgo biloba* L.	Morton	*C. Morton 2010-27* (CM)	EU264210
	Gnetales	Welwitschiaceae	*Welwitschia mirabilis* Hook. f.	University of Pittsburgh Biological Greenhouse	*C. Morton 2010-28* (CM)	EU264213
Angiosperms	Amborellales	Amborellaceae	*Amborella trichopoda* Baill.	2000.0348 (UC, UCBG)	2000.0348 (UC, UCBG)	EU264292
	Chloranthales	Chloranthaceae	*Ascarina* J. R. Forst. & G. Forst., sp. indet.	*Thien 500* (NO)	*L. B. Thien 500* (NO)	EU264260
			Chloranthus multistachys C. Pei	*K. Wurdack 92-0010*	*K. Wurdack 92-0010* (US)	EU264259
	Nymphaeales	Nymphaeaceae	*Brasenia schreberi* J. F. Gmel.	*Qiu 91031* (NCU)	*Y.-L. Qiu 91031* (NCU)	EU264275
			Nuphar lutea (L.) Sm.	81.0800 (UCBG)	81.0800 (UCBG, UC)	EU264293
			Nymphaea L., sp. indet.	*Qiu 91029* (NCU)	*Y.-L. Qiu 91029* (NCU)	EU264262
	Austrobaileyales	Austrobaileyaceae	*Austrobaileya scandens* C. T. White	*Qiu 90030* (NCU)	*Y.-L. Qiu 90030* (NCU)	EU264258
		Schisandraceae	*Kadsura japonica* (L.) Dunal	72.0156 (UCBG)	72.0156 (UC, UCBG)	EU264261
			Schisandra chinensis (Turcz.) Baill.	70.0209 (UCBG)	70.0209 (UC, UCBG)	EU264271
	Ceratophyllales	Ceratophyllaceae	*Ceratophyllum demersum* L.	*C. R. Parks* (IND)	*C. R. Parks* (IND)	EU264214
Magnoliids	Canellales	Canellaceae	*Canella winterana* (L.) Gaertn.	*Qiu 90017* (NCU)	*Y.-L. Qiu 90017* (NCU)	EU264255
		Winteraceae	*Drimys winteri* J. R. Forst. & G. Forst.	*Qiu 90016* (NCU)	*Y.-L. Qiu 90016* (NCU)	EU264254
			Tasmannia insipida R. Br. ex DC.	*Qiu 90032* (NCU)	*Y.-L. Qiu 90032* (NCU)	EU264256
	Laurales	Atherospermataceae	*Atherosperma moschatum* Labill.	*Qiu 92007* (NCU)	*Y.-L. Qiu 92007* (NCU)	EU264257
			Daphnandra micrantha (Tul.) Benth.	*Whalen 132* (NCU)	*Whalen 132* (NCU)	EU264269
			Doryphora sassafras Endl.	*Qiu 98109* (Z)	*Y.-L. Qiu 98109* (Z)	EU264270
		Calycanthaceae	*Calycanthus floridus* L.	65.0164 (UCBG)	65.0164 (UC, UCBG)	EU264294
			Chimonanthus praecox Lindl.	*Qiu 9* (NCU)	*Y.-L. Qiu 9* (NCU)	EU264268
		Gomortegaceae	*Gomortega keule* (Molina) Baill.	2001.0213 (UCBG)	2001.0213 (UC, UCBG)	EU264287
		Hernandiaceae	*Gyrocarpus americanus* Jacq.	96851*A (FTBG)	*C. & A. Morton 2009-17* (CM)	EU264302
			Hernandia sonora L.	DF311*B (FTBG)	*C. & A. Morton 2009-6* (CM)	EU264300
		Lauraceae	*Cinnamomum zeylanicum* Blume	95/0619 (PCPT)	*C. Morton 2010-3* (CM)	EU264303
			Cryptocarya meisneriana Frodin	*Qiu 98048* (Z)	*Y.-L. Qiu 98048* (Z)	EU264272
			Laurus nobilis L.	*Qiu 94209* (IND)	*Y.-L. Qiu 94209* (IND)	EU264273
		Monimiaceae	*Hedycarya arborea* J. R. Forst. & G. Forst.	*Qiu 90028* (NCU)	*Y.-L. Qiu 90028* (NCU)	EU264276
			Hortonia floribunda Wight ex Arn.	*Qiu 02002* (no voucher)	*Y.-L. Qiu 02002* (no voucher)	EU264215
			Kibara coriacea (Blume) Hook. f. & Thomson	*M. Coode 7879* (K)	*M. Coode 7879* (K)	EU264301
		Siparunaceae	*Siparuna brasiliensis* A. DC.	*J. Lombardi 2714* (MO)	*J. Lombardi 2714* (MO)	EU264274

Appendix 1. Continued.

Group	Order	Family	Species	Voucher/Source	Museum voucher/Number	GenBank number
	Magnoliales	Annonaceae	*Annona glabra* L.	63271*B (FTBG)	*C. Morton 2010-38* (CM)	EU264298
			Cananga odorata (Lam.) Hook. f. & Thomson	2001-0325*A (FTBG)	*C. & A. Morton 2009-15* (CM)	EU264267
		Degeneriaceae	*Degeneria roseiflora* John M. Mill.	*J. M. Miller 1189-63* (K)	*J. M. Miller 1189-63* (K)	EU264266
		Eupomatiaceae	*Eupomatia bennettii* F. Muell.	86.0660 (UCBG)	86.0660 (UC, UCBG)	EU264299
		Himantandraceae	*Galbulimima belgraveana* (F. Muell.) Sprague	*P. H. Weston 929* (NSW)	*P. H. Weston 929* (NSW)	EU264297
		Magnoliaceae	*Liriodendron tulipifera* L.	*Isaac 18669* (CM)	*J. & B. Isaac 18669* (CM)	EU264295
			Magnolia acuminata L.	*Isaac 18685* (CM)	*J. & B. Isaac 18685* (CM)	EU264296
		Myristicaceae	*Mauloutchia chapelieri* Warb.	*G. E. Schatz et al. 3847A* (MO)	*G. E. Schatz et al. 3847A* (MO)	EU264264
			Myristica fragrans Houtt.	*Qiu 92014* (NCU)	*Y.-L. Qiu 92014* (NCU)	EU264263
	Piperales	Aristolochiaceae	*Aristolochia maxima* Jacq.	75602*A (FTBG)	*C. & A. Morton 2009-2* (CM)	EU264249
			Asarum canadense L.	*Peter Kuhlman* (IND)	*P. Kuhlman* (IND)	EU264250
			Thottea tomentosa (Blume) Ding Hou	*M. W. Chase 1211* (K)	*M. W. Chase 1211* (K)	EU264251
		Saururaceae	*Anemopsis californica* (Nutt.) Hook. & Arn.	*Qiu 97116* (IND)	*Y.-L. Qiu 97116* (IND)	EU264439
			Houttuynia cordata Thunb.	*Qiu 92016* (NCU)	*Y.-L. Qiu 92016* (NCU)	EU264253
			Saururus cernuus L.	78.0467 (UCBG)	78.0467 (UC, UCBG)	EU264252
Monocots	Acorales	Acoraceae	*Acorus gramineus* Sol. ex Aiton	94.1197 (UCBG)	94.1197 (UC, UCBG)	EU264285
	Alismatales	Araceae	*Orontium aquaticum* L.	*Qiu 97112* (IND)	*Y.-L. Qiu 97112* (IND)	EU264440
		Tofieldiaceae	*Pleea tenuifolia* Michx.	*Qiu 96128* (IND)	*Y.-L. Qiu 96128* (IND)	EU264279
	Asparagales	Xanthorrhoeaceae	*Lomandra obliqua* (Thunb.) J. F. Macbr.	*Qiu 98016* (Z)	*Y.-L. Qiu 98016* (Z)	EU264240
			Xanthorrhoea quadrangulata F. Muell.	*Qiu 97039* (IND)	*Y.-L. Qiu 97039* (IND)	EU264242
	Dioscoreales	Dioscoreaceae	*Dioscorea* L., sp. indet.	97750*A (FTBG)	*C. & A. Morton 2009-4* (CM)	EU264304
			Tacca chantrieri André	*Qiu 01015* (MASS)	*Y.-L. Qiu 01015* (MASS)	EU264278
	Liliales	Smilacaceae	*Smilax china* L.	73.0594 (UCBG)	73.0594 (UC, UCBG)	EU264277
	Pandanales	Cyclanthaceae	*Carludovica palmata* Ruiz. & Pav.	FG4902*A (FTBG)	*C. & A. Morton 2009-1* (CM)	EU264305
		Velloziaceae	*Talbotia elegans* Balf.	61.0758 (UCBG)	61.0758 (UC, UCBG)	EU264280
Commelinids	Arecales	Arecaceae	*Chamaedorea fragrans* Mart.	5875*A (FTBG)	*C. & A. Morton 2009-16* (CM)	EU264306
	Poales	Bromeliaceae	*Vriesea splendens* (Brongn.) Lem.	*Qiu 96073* (IND)	*Y.-L. Qiu 96073* (IND)	EU264239
	Zingiberales	Marantaceae	*Maranta leuconeura* E. Morren	*Qiu 95081* (IND)	*Y.-L. Qiu 95081* (IND)	EU264241
		Strelitziaceae	*Strelitzia nicolai* Regel & K. Koch	77117*A (FTBG)	*C. & A. Morton 2009-10* (CM)	EU264307
Eudicots						
	Buxales	Buxaceae	*Buxus sempervirens* L.	62.0414 (UCBG)	62.0414 (UC, UCBG)	EU264236
			Pachysandra procumbens Michx.	60.1303 (UCBG)	60.1303 (UC, UCBG)	EU264238
	Sabiales	Sabiaceae	*Sabia campanulata* Wall.	94.0765 (UCBG)	94.0765 (UC, UCBG)	EU264316
	Trochondendrales	Trochodendraceae	*Trochodendron aralioides* Siebold & Zucc.	61.0594 (UCBG)	61.0594 (UC, UCBG)	EU264317

Appendix 1. Continued.

Group	Order	Family	Species	Voucher/Source	Museum voucher/Number	GenBank number
	Proteales	Proteaceae	*Platanus orientalis* L.	76.0216 (UCBG)	76.0216 (UC, UCBG)	EU264315
	Ranunculales	Berberidaceae	*Caulophyllum robustum* Maxim.	98.0013 (UCBG)	98.0013 (UC, UCBG)	EU264313
			Nandina domestica Thunb.	no accession listed (PCPT)	*C. Morton 2010-4* (CM)	EU264309
		Eupteleaceae	*Euptelea pleiosperma* Hook. f. & Thomson	74.0757 (UCBG)	74.0757 (UC, UCBG)	EU264314
		Lardizabalaceae	*Decaisnea fargesii* Franch.	2002.0189 (UCBG)	2002.0189 (UC, UCBG)	EU264312
			Lardizabala biternata Ruiz & Pav.	53.116 (UCBG)	53.116 (UC, UCBG)	EU264310
		Papaveraceae	*Eschscholzia californica* Cham.	62.1419 (UCBG)	62.1419 (UC, UCBG)	EU264311
		Ranunculaceae	*Hydrastis canadensis* L.	99.059 (UCBG)	99.059 (UC, UCBG)	EU264232
			Nigella damascena L.	87.0734 (UCBG)	87.0734 (UC, UCBG)	EU264308
	Dilleniales	Dilleniaceae	*Dillenia indica* L.	*Qiu 95129* (IND)	*Y.-L. Qiu 95129* (IND)	EU264233
	Gunnerales	Gunneraceae	*Gunnera magellanica* Lam.	93.1181 (UCBG)	93.1181 (UC, UCBG)	EU264235
			Gunnera monoica Raoul	*Qiu 98071* (Z)	*Y.-L. Qiu 98071* (Z)	EU264234
	Caryophyllales	Cactaceae	*Pereskia portulacifolia* (L.) DC.	8465*A (FTBG)	*C. & A. Morton 2009-3* (CM)	EU264349
		Caryophyllaceae	*Silene nutans* L.	*M. W. Chase 2292* (K)	*M. W. Chase 2292* (K)	EU264352
		Droseraceae	*Drosera binata* Labill.	71.0223 (UCBG)	71.0223 (UC, UCBG)	EU264347
		Nepenthaceae	*Nepenthes northiana* Hook. f.	99.0393 (UCBG)	99.0393 (UC, UCBG)	EU264346
		Nyctaginaceae	*Bougainvillea glabra* Choisy	*M. W. Chase 2485* (K)	*M. W. Chase 2485* (K)	EU264351
		Plumbaginaceae	*Plumbago auriculata* Lam.	87314*A (FTBG)	*C. & A. Morton 2009-12* (CM)	EU264344
		Portulacaceae	*Portulaca grandiflora* Hook.	no accession listed (PCPT)	*C. Morton 2010-5* (CM)	EU264350
			Talinum paniculatum (Jacq.) Gaertn.	90.0939 (UCBG)	90.0939 (UC, UCBG)	EU264348
		Simmondsiaceae	*Simmondsia chinensis* C. K. Schneid.	*Qiu 96120* (IND)	*Y.-L. Qiu 96120* (IND)	EU264345
	Santalales	Santalaceae	*Osyris alba* L.	2002.0996 (UCBG)	2002.0996 (UC, UCBG)	EU264237
Rosids	Crossosomatales	Stachyuraceae	*Stachyurus praecox* Siebold & Zucc.	81.0031 (UCBG)	81.0031 (UC, UCBG)	EU264432
		Staphyleaceae	*Staphylea trifolia* L.	512642 (CM)	*B. & J. Isaac 18690* (CM)	EU264433
	Geraniales	Geraniaceae	*Geranium sanguineum* L.	99/1397A (PCPT)	*C. Morton 2010-6* (CM)	EU264243
		Melianthaceae	*Greyia radlkoferi* Szyszył.	61.1016 (UCBG)	61.1016 (UC, UCBG)	EU264282
	Myrtales	Myrtaceae	*Metrosideros nervulosa* C. Moore & F. Muell.	*M. W. Chase 2451* (K)	*M. W. Chase 2451* (K)	EU264247
			Myrciaria cauliflora (Mart.) O. Berg	95/0621 (PCPT)	*C. Morton 2010-7* (CM)	EU264246
			Psidium littorale Raddi	95/0712 (PCPT)	*C. Morton 2010-8* (CM)	EU264245
		Penaeaceae	*Penaea cneorum* Meerb.	96.0085 (UCBG)	96.0085 (UC, UCBG)	EU264248
	Saxifragales	Altingiaceae	*Liquidambar styraciflua* L.	77.0386 (UCBG)	77.0386 (UC, UCBG)	EU264434
		Cercidiphyllaceae	*Cercidiphyllum japonicum* Siebold & Zucc. ex J. J. Hoffm. & J. H. Schult. bis	93.0206 (UCBG)	93.0206 (UC, UCBG)	EU264442
		Daphniphyllaceae	*Daphniphyllum himalayense* Müll. Arg.	2002.0188 (UCBG)	2002.0188 (UC, UCBG)	EU264443
		Grossulariaceae	*Ribes cynosbati* L.	*S. P. Grund 2313* (CM)	*S. P. Grund 2313* (CM)	EU264437
		Hamamelidaceae	*Corylopsis sinensis* Hemsl.	81.0149 (UCBG)	81.0149 (UC, UCBG)	EU264436

Appendix 1. Continued.

Group	Order	Family	Species	Voucher/Source	Museum voucher/Number	GenBank number
			Hamamelis virginiana L.	*L. Speedy LS-07-387* (CM)	*L. Speedy LS-07-387* (CM)	EU264435
		Iteaceae	*Itea virginica* L.	00/1213 (PCPT)	*C. Morton 2010-9* (CM)	EU264438
		Paeoniaceae	*Paeonia lactiflora* Pall.	512633 (CM)	*B. Isaac 18677* (CM)	EU264441
Eurosids I	Celastrales	Celastraceae	*Celastrus orbiculatus* Thunb.	481520 (CM)	*B. & J. Isaac 9632* (CM)	EU264428
			Euonymus atropurpureus Jacq.	512573 (CM)	*B. & J. Isaac 18687* (CM)	EU264429
			Parnassia palustris L.	2002.065 (UCBG)	2002.065 (UC, UCBG)	EU264430
	Cucurbitales	Begoniaceae	*Begonia* L., sp. indet.	00/0528 (PCPT)	*C. Morton 2010-10* (CM)	EU264460
		Coriariaceae	*Coriaria sarmentosa* G. Forst.	95.0196 (UCBG)	95.0196 (UC, UCBG)	EU264459
		Cucurbitaceae	*Cucumis sativus* L.	Morton	*C. Morton 2010-29* (CM)	EU264458
	Fabales	Fabaceae	*Acacia* Mill., sp. indet.	99/0912 (PCPT)	*C. Morton 2010-11* (CM)	EU264454
			Albizia cubana Britton & P. Wilson	2000124*D (FTBG)	*C. & A. Morton 2009-21* (CM)	EU264455
			Sophora toromiro Skottsb.	*M. W. Chase 747* (K)	*M. W. Chase 747* (K)	EU264456
			Vicia caroliniana Walter	489294 (CM)	*B. & J. Isaac 9682* (CM)	EU264457
		Quillajaceae	*Quillaja saponaria* Molina	36.1419 (UCBG)	36.1419 (UC, UCBG)	EU264453
	Fagales	Betulaceae	*Betula* L., sp. indet.	no accession listed (PCPT)	*C. Morton 2010-12* (CM)	EU264449
		Fagaceae	*Quercus virginiana* Mill.	2000152*A (FTBG)	*C. & A. Morton 2009-25* (CM)	EU264450
		Juglandaceae	*Juglans guatemalensis* W. E. Manning in Standl. & Steyerm.	92.0561 (UCBG)	92.0561 (UC, UCBG)	EU264451
			Platycarya strobilacea Siebold & Zucc.	80.1197 (UCBG)	80.1197 (UC, UCBG)	EU264452
		Myricaceae	*Myrica pensylvanica* Hort. Reg. ex Lam.	99/1372 (PCPT)	*C. Morton 2010-13* (CM)	EU264448
	Malpighiales	Chrysobalanaceae	*Chrysobalanus icaco* L.	99/1920 (PCPT)	*C. Morton* (no voucher)	EU264221
		Clusiaceae	*Clusia* L., sp. indet.	77.0031 (UCBG)	77.0031 (UC, UCBG)	EU264227
		Euphorbiaceae	*Codiaeum variegatum* (L.) Rumph. ex A. Juss.	99/1772 (PCPT)	*C. Morton 2010-15* (CM)	EU264224
			Euphorbia neriifolia L.	96/0677 (PCPT)	*C. Morton 2010-16* (CM)	EU264225
			Euphorbia pseudocactus A. Berger	96/0678 (PCPT)	*C. Morton 2010-17* (CM)	EU264226
			Phyllanthus flexuosus Müll. Arg.	90.0901 (UCBG)	90.0901 (UC, UCBG)	EU264217
		Malpighiaceae	*Byrsonima lucida* DC.	69363*A (FTBG)	*C. & A. Morton 2009-24* (CM)	EU264222
			Malpighia glabra L.	95/0646.A (PCPT)	*C. Morton 2010-18* (CM)	EU264223
		Passifloraceae	*Passiflora suberosa* L.	*S. A. Thompson & J. H. Nishida 2761* (CM)	*S. A. Thompson & J. H. Nishida 2761* (CM)	EU264216
		Salicaceae	*Populus grandidentata* Michx.	492481 (CM)	*B. Isaac & T. Herman 11781* (CM)	EU264220
			Salix alba L.	512624 (CM)	*B. Isaac 18658* (CM)	EU264219
		Violaceae	*Hybanthus prunifolius* (Humb. & Bonpl.) Schulze-Menz	65657*A (FTBG)	*C. & A. Morton 2009-7* (CM)	EU264218
	Oxalidales	Cephalotaceae	*Cephalotus follicularis* Labill.	2001.0116 (UCBG)	2001.0116 (UC, UCBG)	EU264228
		Cunoniaceae	*Cunonia capensis* L.	96.0024 (UCBG)	96.0024 (UC, UCBG)	EU264229

Appendix 1. Continued.

Group	Order	Family	Species	Voucher/Source	Museum voucher/Number	GenBank number
		Elaeocarpaceae	*Crinodendron patagua* Molina	54.1123 (UCBG)	54.1123 (UC, UCBG)	EU264231
		Oxalidaceae	*Averrhoa carambola* L.	Morton	*C. Morton 2010-30* (CM)	EU264230
	Rosales	Cannabaceae	*Celtis* L., sp. indet.	Morton	*C. Morton 2010-31* (CM)	EU264265
			Humulus lupulus L.	512631 (CM)	*B. Isaac 18675* (CM)	EU264283
		Moraceae	*Ficus elastica* Roxb.	99/1907 (PCPT)	*C. Morton 2010-19* (CM)	EU264444
			Morus alba L.	512650 (CM)	*B. Isaac 18660* (CM)	EU264445
		Rhamnaceae	*Rhamnus frangula* L.	512638 (CM)	*B. & J. Isaac 18683* (CM)	EU264447
		Rosaceae	*Rosa* L., sp. indet.	Morton	*C. Morton 2010-32* (CM)	EU264284
			Spiraea japonica L. f.	01/0171 (PCPT)	*C. Morton 2010-20* (CM)	EU264461
		Ulmaceae	*Zelkova serrata* Makino	94.1121 (UCBG)	94.1121 (UC, UCBG)	EU264446
		Urticaceae	*Urtica dioica* L.	99.0492 (UCBG)	99.0492 (UC, UCBG)	EU264281
Eurosids II	Brassicales	Brassicaceae	*Arabidopsis thaliana* (L.) Heynh.	GenBank NC_003075	GenBank NC_003075	
			Capparis spinosa L.	62.0728 (UCBG)	62.0728 (UC, UCBG)	EU264420
		Caricaceae	*Carica papaya* L.	volunteer seedlings (FTBG)	*C. & A. Morton 2009-26* (CM)	EU264421
		Resedaceae	*Reseda luteola* L.	98.0665 (UCBG)	98.0665 (UC, UCBG)	EU264419
		Tropaeolaceae	*Tropaeolum majus* L.	98.0856 (UCBG)	98.0856 (UC, UCBG)	EU264422
	Malvales	Bixaceae	*Bixa orellana* L.	89.0572 (UCBG)	89.0572 (UC, UCBG)	EU264424
		Cistaceae	*Cistus parviflorus* Lam.	2004.0774 (UCBG)	2004.0774 (UC, UCBG)	EU264426
			Helianthemum apenninum Mill.	86.0822 (UCBG)	86.0822 (UC, UCBG)	EU264425
		Dipterocarpaceae	*Hopea odorata* Roxb.	961229*A (FTBG)	*C. & A. Morton 2009-8* (CM)	EU264427
		Malvaceae	*Sterculia urens* Roxb.	*R. Aborn s.n.* (CM)	*R. Aborn s.n.* (CM)	EU264423
	Sapindales	Anacardiaceae	*Pistacia lentiscus* L.	2002.0618 (UCBG)	2002.0618 (UC, UCBG)	EU264431
			Rhus glabra L.	*S. P. Grund & S. V. Parker 3813* (CM)	*S. P. Grund & S. V. Parker 3813* (CM)	EU264400
		Burseraceae	*Bursera inaguensis* Britton	64269*M (FTBG)	*C. & A. Morton 2009-22* (CM)	EU264406
		Meliaceae	*Swietenia macrophylla* King in Hook.	951002*B (FTBG)	*C. & A. Morton 2009-18* (CM)	EU264415
		Rutaceae	*Helietta parvifolia* (A. Gray ex Hemsl.) Benth.	91.0496 (UCBG)	91.0496 (UC, UCBG)	EU264418
			Agathosma ovata (Thunb.) Pillans	*M. W. Chase 1667* (K)	*M. W. Chase 1667* (K)	EU264409
			Bosistoa brassii T. G. Hartley	*M. W. Chase 2492* (K)	*M. W. Chase 2492* (K)	EU264410
			Casimiroa edulis La Llave	*M. W. Chase 1342* (K)	*M. W. Chase 1342* (K)	EU264403
			Citropsis gabunensis Swingle & M. Kellerm.	*C. Morton 3286* (CRC)	*C. Morton 2010-35* (CM)	EU264396
			Eremocitrus glauca (Lindl.) Swingle	*M. W. Chase 1768* (K)	*M. W. Chase 1768* (K)	EU264414
			Fortunella japonica Swingle	*M. W. Chase 1758* (K)	*M. W. Chase 1758* (K)	EU264397
			Melicope ternata J. R. Forst. & G. Forst.	*M. W. Chase 1759* (K)	*M. W. Chase 1759* (K)	EU264401
			Pilocarpus pennatifolius Lem.	*M. W. Chase 1760* (K)	*M. W. Chase 1760* (K)	EU264408
			Poncirus trifoliata (L.) Raf.	*C. Morton 27* (US)	*C. Morton 2010-36* (CM)	EU264398

Appendix 1. Continued.

Group	Order	Family	Species	Voucher/Source	Museum voucher/Number	GenBank number
			Ravenia infelix Vell.	*J. Kallunki et al. 614* (NY)	*J. Kallunki et al. 614* (NY)	EU264411
			Ruta graveolens L.	99/1337 (PCPT)	*C. Morton 2010-21* (CM)	EU264412
			Spathelia excelsa (K. Krause) R. S. Cowan & Brizicky	*M. W. Chase 1899* (K)	*M. W. Chase 1899* (K)	EU264413
			Teclea simplicifolia (Engl.) Engl.	*M. W. Chase 1764* (K)	*M. W. Chase 1764* (K)	EU264417
			Tetradium daniellii (Benn.) T. G. Hartley	*M. W. Chase 633* (K)	*M. W. Chase 633* (K)	EU264416
			Triphasia trifolia P. Wilson	*C. Morton 111G* (IPB)	*C. Morton 2010-33* (CM)	EU264399
			Zanthoxylum monophyllum P. Wilson	*M. W. Chase 332* (K)	*M. W. Chase 332* (K)	EU264402
		Sapindaceae	*Acer rubrum* L.	512646 (CM)	*B. Isaac 18667* (CM)	EU264407
			Aesculus hippocastanum L.	513762 (CM)	*B. & J. Isaac 18671* (CM)	EU264404
		Simaroubaceae	*Ailanthus altissima* (Mill.) Swingle	*H. George s.n.* (CM)	*H. George s.n.* (CM)	EU264405
Asterids	Cornales	Cornaceae	*Cornus mas* L.	01/0151 (PCPT)	*C. Morton 2010-22* (CM)	EU264354
			Nyssa sylvatica Marshall	82.2016 (UCBG)	82.2016 (UC, UCBG)	EU264353
		Hydrangeaceae	*Hydrangea paniculata* Siebold	512623 (CM)	*B. Isaac 18659* (CM)	EU264355
	Ericales	Actinidiaceae	*Clematoclethra lasioclada* Maxim.	*M. W. Chase 596* (K)	*M. W. Chase 596* (K)	EU264325
		Balsaminaceae	*Impatiens repens* Moon	*M. W. Chase 901* (K)	*M. W. Chase 901* (K)	EU264366
		Clethraceae	*Clethra arborea* Aiton	*M. W. Chase 902* (K)	*M. W. Chase 902* (K)	EU264321
		Cyrillaceae	*Cyrilla racemiflora* L.	80.0255 (UCBG)	80.0255 (UC, UCBG)	EU264320
		Diapensiaceae	*Galax urceolata* (Poir.) Brummitt	*M. W. Chase 1449* (K)	*M. W. Chase 1449* (K)	EU264335
		Ebenaceae	*Diospyros digyna* Jacq.	X.3-28*A (FTBG)	*C. & A. Morton 2009-9* (CM)	EU264323
			Diospyros mespiliformis Hochst. ex A. DC.	6190*A (FTBG)	*C. & A. Morton 2009-20* (CM)	EU264322
			Euclea natalensis A. DC.	*P. Goldblatt 9275* (MO)	*P. Goldblatt 9275* (MO)	EU264324
		Ericaceae	*Craibiodendron yunnanense* W. W. Sm.	*M. W. Chase 908* (K)	*M. W. Chase 908* (K)	EU264343
			Rhododendron hippophaeoides Balf. f. & W. W. Sm.	RBG Edinburgh 321022 (E)	*Morton* (no voucher)	EU264319
		Fouquieriaceae	*Fouquieria columnaris* Kellogg ex Curran	*M. W. Chase 269* (NCU)	*M. W. Chase 269* (NCU)	EU264359
			Fouquieria splendens Engelm. in Wisl.	2000202*A (FTBG)	*C. & A. Morton 2009-5* (CM)	EU264361
		Lecythidaceae	*Couroupita guianensis* Aubl.	X.1-489*A, Plot 137 (FTBG)	*C. & A. Morton 2009-14* (CM)	EU264332
		Marcgraviaceae	*Marcgravia rectiflora* Triana & Planch.	*M. W. Chase 331* (NCU)	*M. W. Chase 331* (NCU)	EU264329
			Marcgravia rectiflora Triana & Planch.	941185*A (FTBG)	*Morton* (no voucher)	EU264362
		Pentaphylacaceae	*Ternstroemia impressa* Lundell	*P. Fritsch 282*	*P. W. Fritsch 1771* (CAS)	EU264339
			Ternstroemia stahlii Krug & Urb.	*F. Axelrod 4538* (UPR)	*F. Axelrod 4538* (UPR)	EU264357
		Primulaceae	*Androsace spinulifera* R. Knuth	*M. W. Chase 954* (NCU)	*M. W. Chase 954* (NCU)	EU264327
			Clavija eggersiana Mez	*M. W. Chase 216* (NCU)	*M. W. Chase 216* (NCU)	EU264338
			Clavija euerganea J. F. Macbr.	86197*A (FTBG)	*C. & A. Morton 2009-19* (CM)	EU264363
			Elingamita johnsonii G. T. S. Baylis	*M. W. Chase 958* (K)	*M. W. Chase 958* (K)	EU264358
			Maesa myrsinoides H. Lév.	*M. W. Chase 309* (NCU)	*M. W. Chase 309* (NCU)	EU264330

Appendix 1. Continued.

Group	Order	Family	Species	Voucher/Source	Museum voucher/Number	GenBank number
			Parathesis (A. DC.) Hook. f., sp. indet.	*P. Fritsch 284*	*P. W. Fritsch 1770* (CAS)	EU264365
		Sapotaceae	*Manilkara zapota* (L.) P. Royen	PRC137*B (FTBG)	*C. & A. Morton 2009-11* (CM)	EU264333
			Planchonella novozelandica (F. Muell.) Allan	*P. Fritsch 287*	*P. W. Fritsch 1769* (CAS)	EU264331
		Sarraceniaceae	*Heliamphora heterodoxa* Steyerm.	71.0222 (UCBG)	71.0222 (UC, UCBG)	EU264342
			Sarracenia flava L.	*M. W. Chase 144* (NCB)	*M. W. Chase 144* (NCB)	EU264341
		Styracaceae	*Rehderodendron macrocarpum* Hu	*M. W. Chase 911* (K)	*M. W. Chase 911* (K)	EU264340
			Styrax japonicus Siebold & Zucc.	*M. W. Chase 974* (K)	*M. W. Chase 974* (K)	EU264336
		Symplocaceae	*Symplocos costata* Choisy ex Zoll.	*M. W. Chase 1374* (K)	*M. W. Chase 1374* (K)	EU264337
			Symplocos paniculata Miq.	*M. W. Chase 913* (K)	*M. W. Chase 913* (K)	EU264360
		Tetrameristaceae	*Pelliciera rhizophorae* Planch. & Triana	*R. T. Pennington et al. 586*	*R. T. Pennington et al. 586* (E)	EU264318
			Tetramerista Miq., sp. indet.	*M. Coode 7925* (K)	*M. Coode 7925* (K)	EU264326
		Theaceae	*Cleyera japonica* Thunb.	*M. W. Chase 1690* (K)	*M. W. Chase 1690* (K)	EU264364
			Eurya japonica Thunb.	*M. W. Chase 1448* (K)	*M. W. Chase 1448* (K)	EU264328
			Schima superba Gardner & Champ.	*Lammers s.n.* (F)	*Lammers s.n.* (F)	EU264356
			Stewartia pseudocamellia Maxim.	*M. W. Chase 984* (K)	*M. W. Chase 984* (K)	EU264334
Euasterids I		Boraginaceae	*Borago officinalis* L.	73.0653 (UCBG)	73.0653 (UC, UCBG)	EU264371
	Garryales	Eucommiaceae	*Eucommia ulmoides* Oliv.	86.128 (UCBG)	86.128 (UC, UCBG)	EU264381
		Garryaceae	*Garrya elliptica* Douglas ex Lindl.	64.1209 (UCBG)	64.1209 (UC, UCBG)	EU264382
	Gentianales	Apocynaceae	*Nerium oleander* L.	78779*B (FTBG)	*C. & A. Morton 2009-23* (CM)	EU264377
		Gelsemiaceae	*Gelsemium sempervirens* (L.) J. St.-Hil.	92.032 (UCBG)	92.032 (UC, UCBG)	EU264383
		Loganiaceae	*Strychnos nux-vomica* L.	*M. W. Chase 2538*	*M. W. Chase 2538*	EU264369
		Rubiaceae	*Coffea arabica* L.	99/0283 (PCPT)	*C. Morton 2010-23* (CM)	EU264367
			Luculia gratissima Wall.	54.1342 (UCBG)	54.1342 (UC, UCBG)	EU264384
	Lamiales	Bignoniaceae	*Catalpa bignonioides* Walter	512590 (CM)	*B. & J. Isaac 18672* (CM)	EU264375
		Calceolariaceae	*Calceolaria tomentosa* Ruiz & Pav.	36.1783 (UCBG)	36.1783 (UC, UCBG)	EU264286
		Gesneriaceae	*Saintpaulia grotei* Engl.	53.0387 (UCBG)	53.0387 (UC, UCBG)	EU264376
		Plantaginaceae	*Antirrhinum* L., sp. indet.	no accession listed (PCPT)	*C. Morton 2010-24* (CM)	EU264368
			Erinus alpinus L.	00/0568 (PCPT)	*C. Morton 2010-25* (CM)	EU264288
	Solanales	Convolvulaceae	*Ipomoea batatas* (L.) Lam.	88.056 (UCBG)	88.056 (UC, UCBG)	EU264386
		Montiniaceae	*Montinia caryophyllacea* Thunb.	75.0110 (UCBG)	75.0110 (UC, UCBG)	EU264379
		Solanaceae	*Solanum carolinense* L.	380780 (CM)	*B. Isaac & C. Chuey 4574* (CM)	EU264370
Euasterids II	Bruniales	Bruniaceae	*Berzelia lanuginosa* (L.) Brongn.	96.0009 (UCBG)	96.0009 (UC, UCBG)	EU264380
	Escalloniales	Escalloniaceae	*Escallonia viscosa* Forbes	54.0058 (UCBG)	54.0058 (UC, UCBG)	EU264394
	Apiales	Apiaceae	*Apium graveolens* L.	*B. Isaac 18674* (CM)	*B. Isaac 18674* (CM)	EU264378
			Heteromorpha arborescens Cham. & Schltdl.	76.0712 (UCBG)	76.0712 (UC, UCBG)	EU264385
			Hydrocotyle verticillata Thunb.	82.1355 (UCBG)	82.1355 (UC, UCBG)	EU264291

Appendix 1. Continued.

Group	Order	Family	Species	Voucher/Source	Museum voucher/Number	GenBank number
		Araliaceae	*Hedera* L., sp. indet.	Morton	*C. Morton 2010-34* (CM)	EU264372
			Panax quinquefolius L.	86.1138 (UCBG)	86.1138 (UC, UCBG)	EU264289
		Pittosporaceae	*Pittosporum daphniphylloides* Hayata	75.0918 (UCBG)	75.0918 (UC, UCBG)	EU264290
	Aquifoliales	Aquifoliaceae	*Ilex glabra* A. Gray	99/1498 (PCPT)	*C. Morton 2010-26* (CM)	EU264373
		Helwingiaceae	*Helwingia japonica* (Thunb.) F. Dietr.	2001.0229 (UCBG)	2001.0229 (UC, UCBG)	EU264374
	Asterales	Asteraceae	*Centaurea montana* L.	87.0398 (UCBG)	87.0398 (UC, UCBG)	EU264395
		Campanulaceae	*Campanula rapunculus* L.	99.0118 (UCBG)	99.0118 (UC, UCBG)	EU264393
		Stylidiaceae	*Stylidium adnatum* R. Br.	71.0519 (UCBG)	71.0519 (UC, UCBG)	EU264392
	Dipsacales	Adoxaceae	*Viburnum prunifolium* L.	512643 (CM)	*B. & J. Isaac 18691* (CM)	EU264390
		Caprifoliaceae	*Dipelta yunnanensis* Franch.	99.045 (UCBG)	99.045 (UC, UCBG)	EU264387
			Lonicera japonica Thunb. ex Murray	BED427 (UCBG)	BED427 (UC, UCBG)	EU264389
			Patrinia scabiosifolia Link	93.1081 (UCBG)	93.1081 (UC, UCBG)	EU264391

Abbreviations used for the following botanical gardens: CM, Carnegie Museum of Natural History Herbarium; CRC, Citrus Genetic Resources, Riverside; FTBG, Fairchild Tropical Botanic Garden; IPB, Bogor Botanical Garden; PCPT, Phipps Conservatory and Botanical Gardens; UCBG, University of California Botanical Garden at Berkeley. Other abbreviations follow Index Herbariorum.

REVISION OF PALEOTROPICAL *MEGALASTRUM* (DRYOPTERIDACEAE)[1]

Germinal Rouhan[2,3] *and Robbin C. Moran*[3]

Abstract

We recognize three species of *Megalastrum* Holttum (Dryopteridaceae) in Africa, the Comoros, Madagascar, Mauritius, and La Réunion. A key to distinguish the three species is provided as well as description, complete synonymy, discussion, specimens examined, and illustration of each species. Two names are excluded from the genus.

Key words: Africa, Comoros, Dryopteridaceae, ferns, Indian Ocean, Madagascar, Mascarene Islands, *Megalastrum*, pteridophytes, systematics, taxonomy.

This paper treats the species of *Megalastrum* Holttum (Dryopteridaceae) occurring in continental Africa, the Comoros, Madagascar, Mauritius, and La Réunion. These are the only areas where the genus is known in the Paleotropics. We estimate that *Megalastrum* contains about 83 species worldwide, some as yet undescribed. The present work is the fifth in a series of papers treating the genus in large geographic regions. The four previous articles published in this series are treatments of the 18 species of *Megalastrum* in Brazil, Paraguay, and Uruguay (Moran et al., 2009a), the nine species in the West Indies (Moran et al., 2009b), the 21 species in Central America (Moran & Prado, 2010), and the seven species in the circumaustral region (Sundue et al., 2010). A separate treatment is underway for South America. Between any two of these regions there is little or no geographic overlap of species.

For a review of the taxonomic history and geography of *Megalastrum*, see Smith and Moran (1987) and Moran et al. (2009a). Christensen (1913, 1920) was the first to point out the distinctiveness of the group. He noted its characteristic laminar cutting and venation; namely, as one goes distally along the pinna, the basal basiscopic pinnules gradually become decurrent and broadly adnate to the pinna rachis. Correspondingly, the vein that supplies the broadly adnate segment or lobe arises from the pinna rachis, not the costule. Among ferns, this combined cutting and venation pattern is noteworthy. Christensen (1913, 1920) pointed out that the form of the hairs on the adaxial surfaces of pinna rachises was a helpful characteristic in identification. Generally, these hairs are coarse, whitish, septate, acicular, and antrorsely or patently strigose (Smith & Moran, 1987). After drying, they often remain terete, the cells not collapsing and twisting at right angles to each other (also observed in the genus *Ctenitis* (C. Chr.) C. Chr.). A distinctive character of *Megalastrum* is that the veins in almost all species end before the laminar margins in enlarged tips (hydathodes). This type of vein termination is uncommon among dryopteroid ferns, which typically have slender vein tips that reach the margin. The Paleotropical *M. lanuginosum* (Willd. ex Kaulf.) Holttum is atypical in the genus by having slender vein tips that extend near or all the way to the laminar margin.

The above characteristics were first pointed out by Christensen (1913: 82–84, 1920: 31–32, 59–60), who treated the species now classified in *Megalastrum* as the "group of *D.* [*Dryopteris*] *subincisa*" of subgenus *Ctenitis* C. Chr. in *Dryopteris* Adans. He assigned about 30 Neotropical species to the group but did not treat the Paleotropical species. Holttum (1983) published a study of *Ctenitis* for the Mascarene Islands, distinguishing three species in

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section *Subincisae* (C. Chr.) Tindale (*C. lanuginosa* (Willd. ex Kaulf.) Copel., *C. canacae* Holttum, and *C. lanata* (Fée) Holttum), but without citing any specimens. Later, Holttum published *Megalastrum* as a new genus (1986), recognizing five Paleotropical species (no infraspecific taxa), but he did not provide a treatment for them (no key or descriptions). Since Holttum's work, no further comprehensive study has been published for the Paleotropical species of *Megalastrum*.

The purpose of our study was to review the species of *Megalastrum* throughout Africa and the western Indian Ocean region, to examine relevant types, and to provide a new taxonomic treatment.

Material and Methods

Herbarium specimens were requested on loan from 16 herbaria: AAU, B, BOL, BR, GH, HBG, K, MICH, MO, NBG, NY, P, PRE, S, US, and WAG. A complete listing of voucher specimens is provided in Appendix 1. To produce the distribution map, the geographic coordinates had to be estimated for most of the specimens because this information was not provided on most labels. Our estimates of geographic coordinates are given in brackets in the Specimens Examined section. The dot distribution map was generated in the geographic information system (GIS) laboratory at the New York Botanical Garden.

Results

Three species, with no infraspecific taxa, are here recognized for the Paleotropics. The first species, *Megalastrum lanuginosum*, has the widest distribution (Fig. 1). The distribution is disjunct in three areas: (1) the western Indian Ocean area (Madagascar, the Comoros, La Réunion, and Mauritius), (2) southern and eastern Africa, and (3) the islands of the Gulf of Guinea in western Africa (Bioko and São Tomé). Similar disjunctions are known for other ferns like *Grammitis nigrocincta* Alston, *Trichomanes digitatum* Sw., and *Antrophyum immersum* (Bory ex Willd.) Hook. & Baker (Figueiredo & Gascoigne, 2001). The two other species, *M. canacae* (Holttum) Holttum and *M. lanatum* (Fée) Holttum, are narrow endemics, occurring only in the Mascarene Islands (La Réunion and Mauritius) and in La Réunion, respectively.

According to preliminary results of molecular phylogeny (unpublished data), the two endemic species to the Mascarene Islands (*Megalastrum canacae* and *M. lanatum*) constitute a clade that is sister to the rest of the genus. Both species share fenestrate perispores, a character unique in the genus (pers. obs.). In contrast, *M. lanuginosum* belongs to a clade of Brazilian species and was resolved sister lineage to *M. crenulans* (Fée) A. R. Sm. & R. C. Moran. The two species share three characters that are rare elsewhere in the genus: bullate scales on the lamina axes, indusiate sori, and veins that extend to the margins (or nearly so) and are nonhydathodous.

Megalastrum Holttum, Gard. Bull. Singapore 39: 161. 1986. TYPE: *Megalastrum villosum* (L.) Holttum [≡ *Polypodium villosum* L.].

Dryopteris Adans. subg. *Ctenitis* C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Math. Afd. ser. 8, 6: 32, 59. 1919 [1920], as "restricted to the species group of *D. subincisa* C. Chr."

Dryopteris sect. *Subincisae* C. Chr., Index Fil., Suppl. 3, 7. 1934. *Ctenitis* C. Chr. sect. *Subincisae* (C. Chr.) Tindale, Contr. New South Wales Natl. Herb. 3: 252. 1965. TYPE: *Dryopteris subincisa* (Willd.) Urb., 1903 [≡ *Polypodium subincisum* Willd., 1810].

Plants terrestrial; rhizomes erect to decumbent; petioles scaly toward the base, with 4 to 10 vascular bundles, the 2 adaxial bundles enlarged; laminae 1-pinnate-pinnatifid ranging to 4-pinnate-pinnatifid, catadromic above the basal pinnae; basal pinnae inequilateral and enlarged on the basiscopic side or (less commonly) equilateral; rachises, pinna rachises, and costules not grooved or only shallowly so, scaly and pubescent abaxially, densely pubescent on the adaxial surfaces, the hairs whitish, spreading to antrorsely strigose, multicellular, if glands present, these ca. 0.1 mm wide, spherical, shiny, yellowish to orangish clear, sessile to stalked; basal basiscopic segment of pinnules becoming decurrent and adnate to the pinna rachises, the vein supplying the segment springing from the pinna rachis instead of the costule; hydathodes present or (more rarely) absent; indusia absent or (less commonly) present, circular, brown, firm, in some species minute and fugacious; spores monolete, nongreen, the perispores cristate or spiny, nonfenestrate or rarely so (2 species); $x = 41$ (Kramer & Green, 1990).

Etymology. The name *Megalastrum* is taken from the Greek "mega-," meaning "large," and "-*Lastrea*," which refers to the genus *Lastrea* Bory named after the French botanist Charles Jean Louis Delastre (1792–1859). When *Ctenitis* was first published (as a subgenus of *Dryopteris*), it included species now placed in *Ctenitis*, *Megalastrum*, and *Triplophyllum* Holttum. Christensen later (1919) recognized four informal species groups within the subgenus, one of which he called the "Group of *D. subincisa*." This group is the same as what we are calling *Megalastrum*.

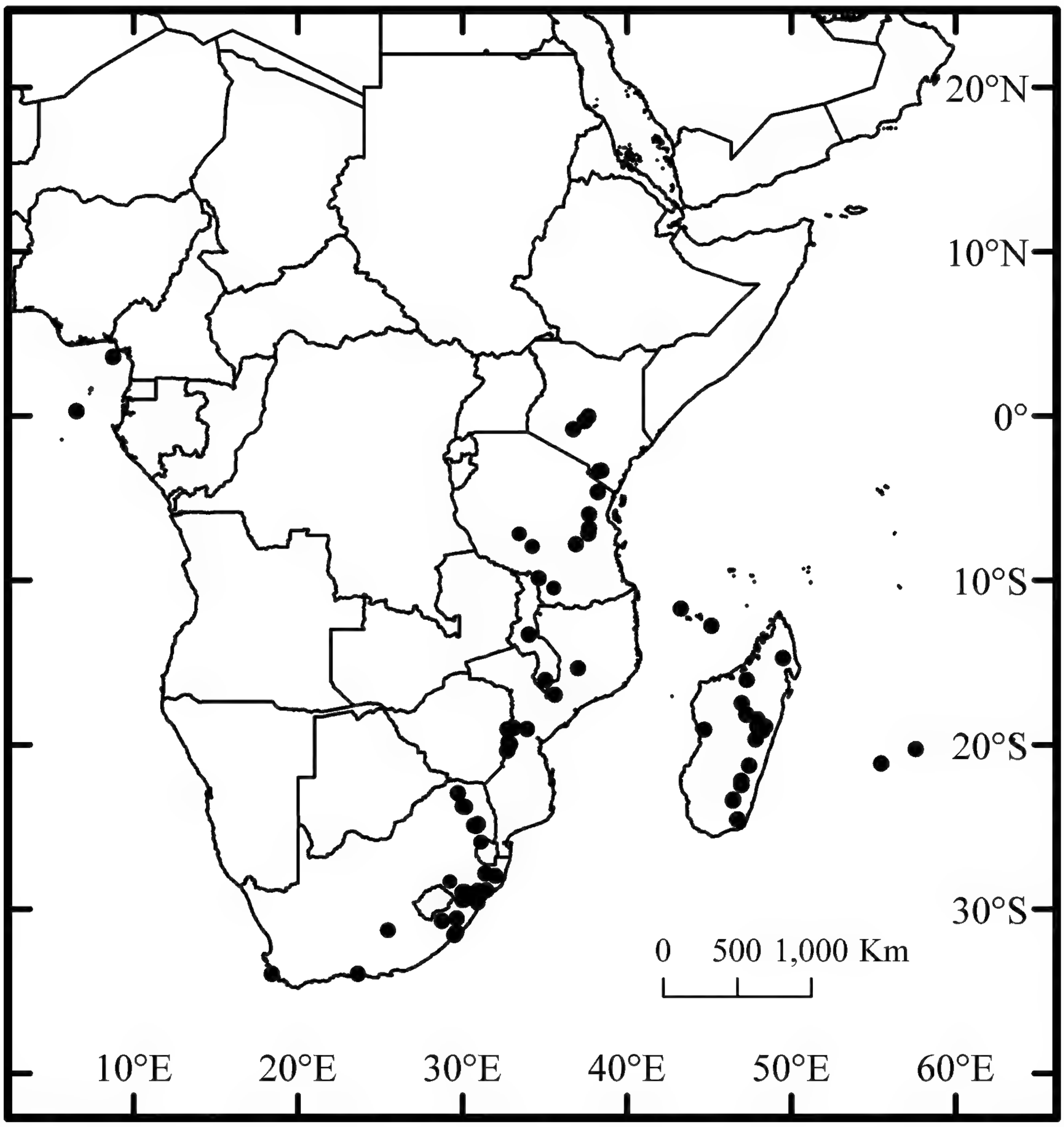

Figure 1. Disjunct distribution of *Megalastrum lanuginosum* between tropical West Africa, where restricted to Bioko and São Tomé, and the eastern Africa and Madagascan region. Black dots indicate the vouchered occurrence of the species.

KEY TO THE SPECIES OF *MEGALASTRUM* IN AFRICA, MADAGASCAR, THE COMOROS, LA RÉUNION, AND MAURITIUS

1a. Rhizome scales golden brown, denticulate; laminae tripinnate-pinnatifid or more divided at the base; indusia conspicuous and persistent, large, to 1.5 mm diam.; bullate scales sparse to abundant on costules and smaller axes abaxially ..... 3. *M. lanuginosum*

1b. Rhizome scales dark brown, subentire; laminae bipinnate-pinnatisect or less divided at base; indusia 0.3–0.5 mm diam. or absent; bullate scales absent on costules and lesser axes.

2a. Lamina on both surfaces between veins glabrous; indusia persistent; hairs of the pinna rachises 0.2–0.5 mm long on the abaxial surfaces, 0.8–1.2 mm long on the adaxial surfaces; hairs of the abaxial surfaces of costules 0.1–0.4 mm long ..... 1. *M. canacae*

2b. Lamina on both surfaces between veins pubescent; indusia absent (rarely present and if so, fugacious); hairs of the pinna rachises 0.5–1.2 mm long on the abaxial surfaces, 1.2–1.7 mm long on the adaxial surfaces; hairs of the abaxial surfaces of costules 0.3–0.6 mm long ..... 2. *M. lanatum*

1. Megalastrum canacae (Holttum) Holttum, Gard. Bull. Singapore 39: 161. 1986 [1987]. Basionym: *Ctenitis canacae* Holttum, Kew Bull. 38: 128. 1983. TYPE: Mauritius. Canaca [20°24′11″S, 57°30′42″E], 1868, *H. Barkly s.n.* (holotype, K!). Figures 2M–T, 3A.

Rhizomes erect, scaly, the scales to 35 mm; fronds to 2.5 m; scales of petiole bases 10–15 × 1–1.5(–2)

mm, linear, subentire, dark brown, spreading to ascending; rachises with similar scales but often much less densely scaly; laminae to 1.2 m, bipinnate-pinnatisect at base, bipinnate-pinnatifid medially; basal pinnae 25–50 cm, the stalks to 2 cm, inequilateral, the pinnules on the acroscopic side slightly reduced toward pinna bases, the 2 or 3 first basiscopic pinnules with lobes pinnatifid and obtuse to rounded apices; pinna rachises abaxially puberulent and ± densely glandular, the hairs erect, 0.2–0.5 mm, 3- to 5-celled, the glands spherical, sessile, ca. 0.1 mm diam., 1-celled, scaly, the scales 4–7(–10) × 0.3–0.5(–1) mm, linear, entire, flat (nonbullate), dark brown, adaxially densely pubescent, the hairs spreading, 0.8–1.2 mm, 5- to 7-celled, septate, nonglandular; costules abaxially puberulent, the hairs spreading to somewhat antrorse, 0.1–0.4 mm, 1- to 3-celled, glands like those on pinna rachises but fewer, scaly, the scales 1.5–3.5 × 0.2–0.4 mm, flat, entire, brown, adaxially pubescent, the hairs antrorse, 0.6–1 mm, 5- to 7-celled, eglandular, septate; laminar tissue between veins glabrous on both surfaces, abaxially sparsely glandular, the glands spherical, sessile; veins to 8 pairs per pinnule lobe, visible on both surfaces, ending before laminar margins in enlarged clavate tips, as conspicuous hydathodes, abaxially sparsely glandular and puberulent, the hairs 0.1–0.4 mm, 2- or 3-celled, adaxially eglandular, puberulent to glabrous, the hairs ca. 0.3–0.5 mm, 3- to 5-celled; laminar margins sparsely ciliate, the hairs ca. 0.3–0.5 mm, 2- or 3-celled; indusia present, persistent (rarely deciduous), circular, 0.3–0.5 mm, pubescent, the hairs 0.1–0.3 mm, 1- or 2-celled, also present on the margins; spores monolete, the perispores fenestrate with short spines on arms between the fenestrae.

Distribution and ecology. *Megalastrum canacae* is a terrestrial fern, found in shady stations of wet mesotherm forests, in ravines, at about 1200 m. The taxon is rare in Mauritius and La Réunion. It is either very rare or possibly now extinct in Mauritius, where it was last collected in 1985 by W. Strahm (collection number 20906), who wrote on the herbarium label "only a few individuals, rare." The only other known locality in Mauritius is Trou Kanaka, where it has not been collected since 1868, although it was searched for at this locality in the early 1980s (Holttum, 1983).

Etymology. The specific epithet *canacae* refers to the crater Kanaka (or Canaca) in Mauritius, where the type specimen was collected.

Discussion. *Megalastrum canacae* is the only species of the genus in the Paleotropics with glabrous laminar tissue between veins on both faces. Other useful characters for distinguishing this species are the numerous dark brown scales that extend from the petiole to the rachis, the antrorse hairs on the adaxial surfaces of the costules and veins, and the persistent indusia.

Contrary to Holttum's statement (1983), the basal basiscopic pinnules of basal pinnae are not necessarily significantly shorter than those next to them. Thus, examining additional specimens, especially recent collections from La Réunion, this character does not appear to distinguish the species. The density of spherical glands observed on the abaxial surfaces can vary among specimens from almost none (*E. Grangaud 4, 5, 1824*) to many (*H. Barkly s.n.*, the holotype). With few exceptions where indusia are extremely reduced and present on only a few pinnules (*E. Grangaud 5* and *1243bis*), indusia are conspicuous, even when dried and shriveled on dried specimens.

Additional specimens examined. MAURITIUS. s. loc., s.d., *W. Bojer s.n.* (K); s. loc., 1871, *W. Cattell s.n.* (NY); s. loc., s.d., *s. coll. 787* (P); s. loc., s.d., *s. coll.* (K); s. loc., 1827, *F. W. Sieber 36* (BR, HBG, HBG photo at MO and K, MO, NY, P); s. loc., 1827, *F. W. Sieber s.n.* (P); Brise Fer, [20°22′35″S, 57°25′28″E], *W. Strahm 20906* (K). LA RÉUNION. s. loc., 1875, *I. B. Balfour s.n.* (K); s. loc., s.d., *J. Potier s.n.* (P). **Saint-Benoît:** Plaine des Palmistes, ravine du Grand Bras Piton, [21°7′0″S, 55°38′0″E], *E. Grangaud 1547* (P). **Saint-Pierre:** Le Dimitile, sentier de la Grande Jument, [21°10′0″S, 55°29′0″E], *E. Grangaud 1243bis* (P); Entre-Deux, Le Dimitile, piste 4 × 4 de la Chapelle, petite ravine dans la partie proche de la piste, [21°10′0″S, 55°29′0″E], *E. Grangaud & M.-F. Grangaud 4, 5, 1824* (P).

2. Megalastrum lanatum (Fée) Holttum, Gard. Bull. Singapore 39: 161. 1986 [1987]. Basionym: *Phegopteris lanata* Fée, Mem. Foug., Gen. Fil. 246. 1850. *Ctenitis lanata* (Fée) Holttum, Kew Bull. 38: 129, 130. 1983. TYPE: La Réunion. s.d., *De Montbrison s.n.* (holotype, P 00483090!). Figures 2G–L, 3B.

Phegopteris montbrisoniana Fée, Mem. Foug., Gen. Fil. 247. 1850. TYPE: "Habitat in insula Borboniâ" [La Réunion], s.d., *De Montbrison s.n.* (holotype, P 00610771!).

Aspidium oppositum Kaulf. ex Spreng. var. *subglandulosum* Mett. ex Kuhn, Filic. Afr. 138. 1868, nom. nud.

Rhizomes short-creeping, scaly, the scales to 20 mm; fronds to 2 m; scales at petiole bases 8–11 × 0.8–2(–3) mm, linear, subentire, dark brown, spreading; rachises with a few, similar but smaller scales in the proximal half; laminae to 1.2 m, deltate, bipinnate-pinnatifid at base and medially; basal pinnae 18–30 cm, the stalks to 1.5 cm, inequilateral, the pinnules on the acroscopic side slightly reduced toward the base of the pinna, the first basiscopic

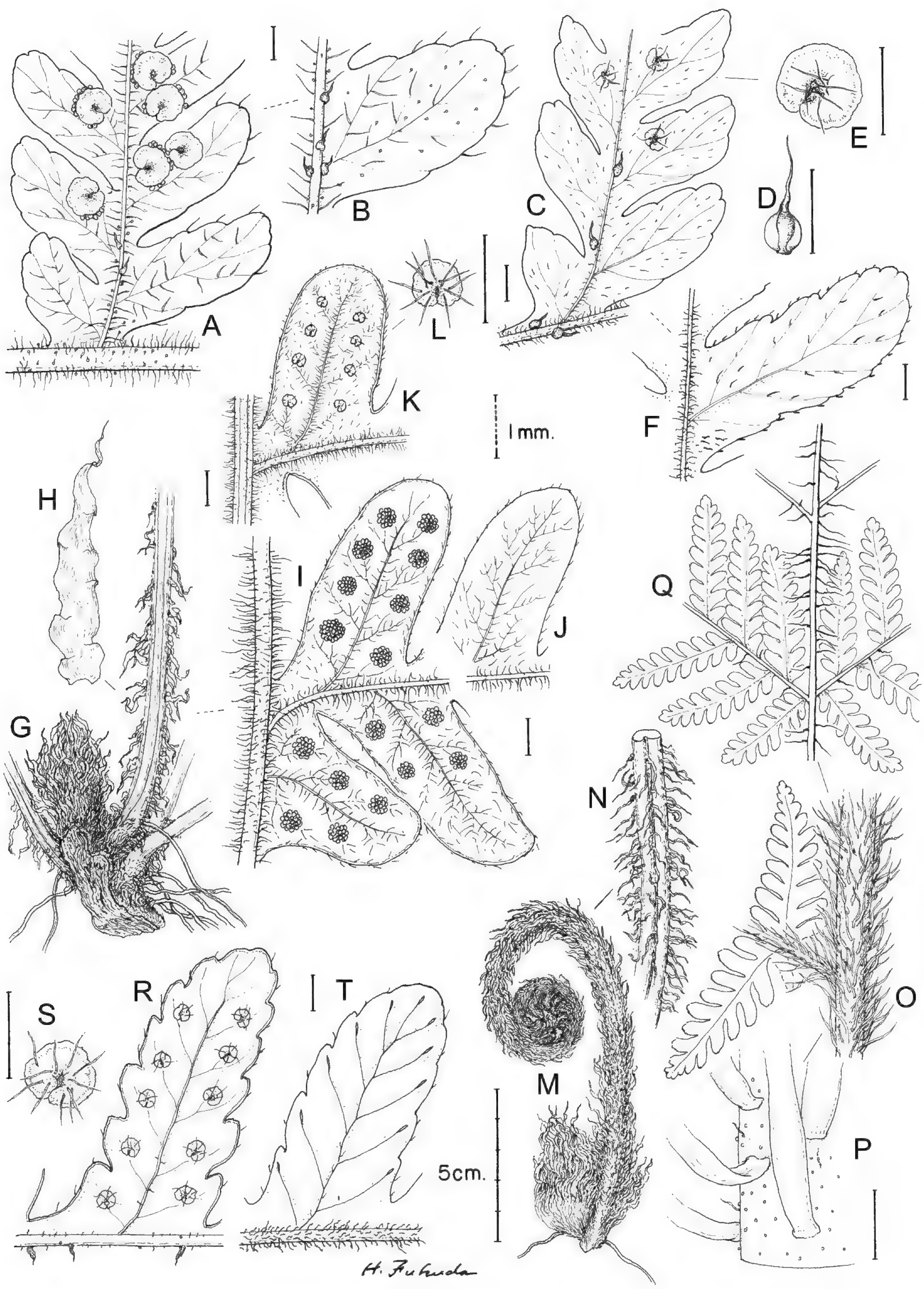

Figure 2. Indument characteristics of the three Paleotropical species of *Megalastrum*. A–F. *M. lanuginosum*. —A. Abaxial surface of pinnule. —B. Abaxial surface of lobe. —C. Abaxial surface of pinnule. —D. Bullate scale from abaxial surface of costule. —E. Indusium. —F. Adaxial surface of lobe. Note veins extending to laminar margin. G–L. *M. lanatum*. —G. Rhizome apex. —H. Rhizome scale. —I. Abaxial surface of pinnule. —J. Abaxial surface of lobe. —K. Abaxial surface of lobe. —L. Indusium. M–T. *M. canacae*. —M. Crozier. —N. Petiole base. —O. Rachis and basal pinnules. —P. Rachis with scale bases and sessile glands. —Q. Adaxial medial pinnae. —R. Abaxial surface of lobe. —S. Indusium. —T. Adaxial

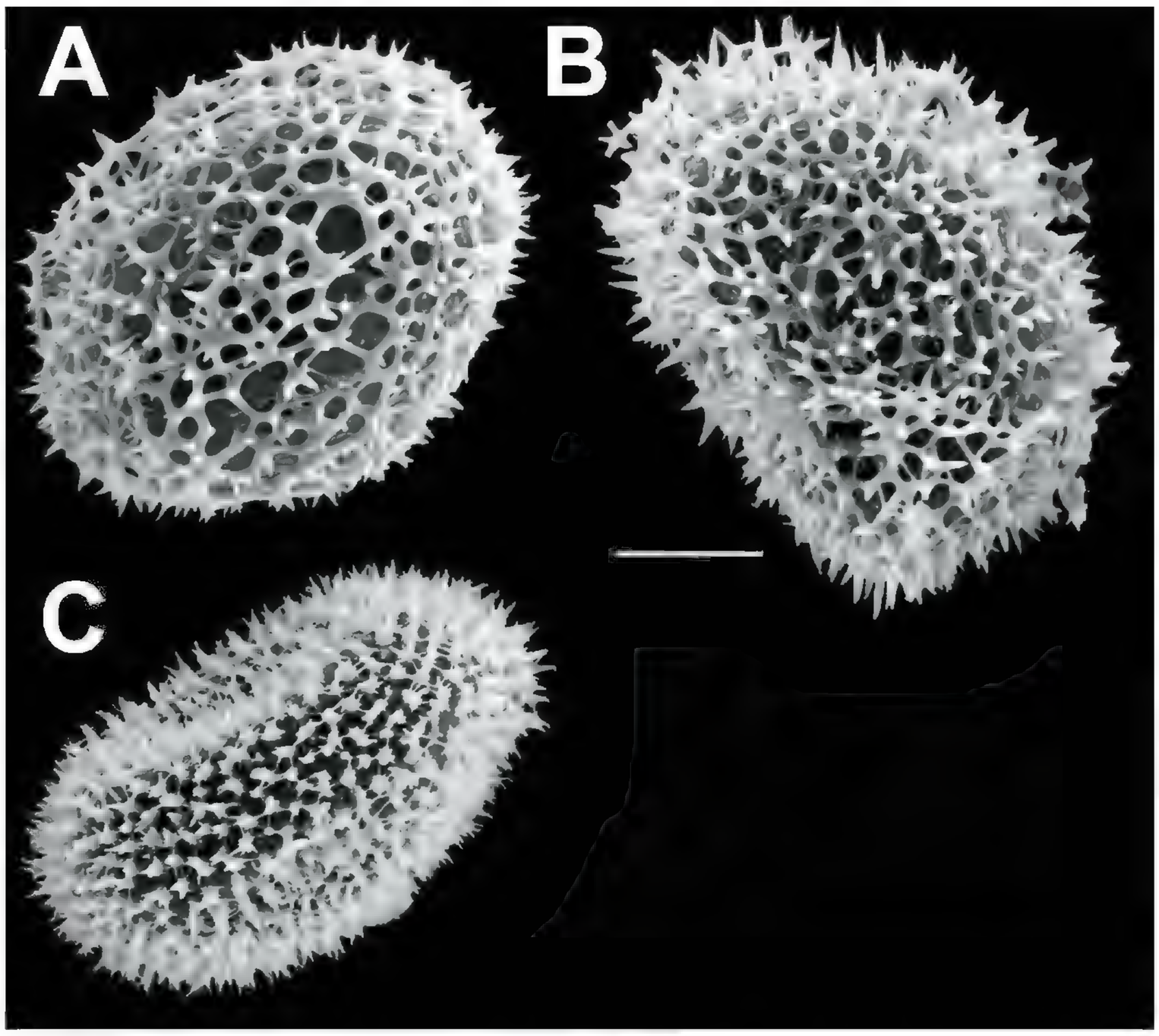

Figure 3. Spores of *Megalastrum*. —A. *M. canacae*, *I. B. Balfour s.n.* (K). —B. *M. lanatum*, *E. Grangaud 7* (P) from La Réunion. —C. *M. lanuginosum*, *L. E. Taylor 754* (NY). Scale bar = 10 μm.

pinnules with lobes lobulate, other pinnules with lobes crenate to subentire toward the apex of the pinna; pinna rachises abaxially pubescent, eglandular, the hairs erect, 0.5–1.2 mm, to 6-celled, scaly, the scales 2–4 × 0.2–0.5 mm, linear, entire, flat (nonbullate), dark brown, adaxially densely pubescent, the hairs erect, 1.2–1.7 mm, 6- to 8-celled, septate, nonglandular; costules abaxially puberulent, eglandular, the hairs spreading to erect, 0.3–0.6 mm, 3- to 5-celled, scaly, the scales 0.3–0.7 × ca. 0.2 mm, flat, entire, adaxially densely pubescent, the hairs erect to spreading, 0.6–1(–1.5) mm, 5- to 7-celled, eglandular, septate; laminar tissue between veins pubescent on both surfaces, abaxially rarely glandular, the glands spherical, sessile, clear or yellowish translucent, to 0.1 mm diam., hairs erect to spreading on both surfaces, 0.3–0.6 mm, 3- to 5-celled; veins to 7 pairs per pinnule lobe, visible on both surfaces, ending before laminar margins in enlarged clavate tips as conspicuous hydathodes, pubescent with hairs like those of the laminar tissue; laminar margins sparsely ciliate, the hairs similar to those of the laminar surfaces; indusia absent, or if present (rarely), reduced, pubescent, pale brown, dull, to 0.5 mm diam., hairs mostly on the margins, ca. 0.5 mm; spores monolete, the perispores fenestrate with short spines on arms between the fenestrae.

Distribution and ecology. *Megalastrum lanatum* is endemic to La Réunion, where it is terrestrial in wet forests, 750–1550 m. Although one specimen (*J. N. Bréon s.n.*, 1834) has "Madagascar" written on it, we believe this to be an error. There is no other collection of *M. lanatum* from Madagascar, and Bréon collected *M. lanatum* in La Réunion in the same year.

Etymology. The species epithet is taken from the Latin word "lana," meaning "wool," referring to the conspicuous, dense, whitish pubescence evident on both faces of the laminae.

←

surface of lobe. Note veins ending before the margin. Structures are drawn from the following collections: *E. A. C. L. E. Schelpe 5375* (BOL) from South Africa (A); *A. J. Whellan 219* (NY) from South Africa (B); *R. B. Faden et al. 72/190* (BOL) from Kenya (C–F); *F. Badré 914bis* (P) from La Réunion (G–K); *L. H. Boivin 884* (P) from La Réunion (L, M); *E. Grangaud 4* (P) from La Réunion (N, O); *H. Barkly s.n.* (K) from Mauritius (P–R); *F. W. Sieber 36* (P) from Mauritius (S, T). Scale bars: A–M, P–T = 1 mm; N, O = 5 cm.

Discussion. *Megalastrum lanatum* differs from *M. canacae* by the laminae between veins pubescent on both surfaces and longer hairs on the pinna rachises and abaxial surfaces of costules. The lack of indusia distinguishes *M. lanatum* from the other two species of the Old World; however, small indusia can be rarely found on a few specimens. Also, indusia may be present but fugacious, and thus only rarely observed. When present, indusia are very reduced, pubescent, and often almost completely hidden by sporangia, with the only evidence of their presence being the marginal hairs that exceed the sporangia.

As noted for *Megalastrum canacae*, recent observations and collections made in La Réunion demonstrate that the length of the basal basiscopic pinnules of basal pinnae is not necessarily shorter than the pinnules next to them, as was claimed by Holttum (1983).

Additional specimens examined. LA RÉUNION. s. loc., s.d., *I. B. Balfour s.n.* (K); s. loc., 1850, *C. Bernier 92* (K); s. loc., s.d., *H. Blanchard s.n.* (US); s. loc., s.d., *L. H. Boivin s.n.* (P); s. loc., 1834, *J. N. Bréon s.n.* (P); s. loc., s.d., *De Montbrison s.n.* (P); s. loc., s.d., *I.? Garnier s.n.* (BR); s. loc., s.d., *C. Gaudichaud s.n.* (P); s. loc., 1844, *J. A. I. Pancher s.n.* (K); s. loc., s.d., *J. M. C. Richard 46* (P); s. loc., 4 Mar. 1847, *s. coll. s.n.* (P). **St. Benoît:** Salazie, sentier vers La Nouvelle, [21°4′0″S, 55°25′0″E], *F. Badré 1052* (P); Salazie, [21°3′0″S, 55°30′0″E], s.d., *L. H. Boivin 122* (BR); Petite Plaine des Palmistes, [21°8′59″S, 55°36′34″E], *T. Cadet 4345* (K); Plaine des Palmistes, [21°7′0″S, 55°38′0″E], *M. G. De L'Isle 429* (K, P); en limite de St. Benoît et Salazie, Forêt de Bélouve, sentier du Mazerin, en bas de pente du coteau Monique, [21°2′0″S, 55°33′0″E], *E. Grangaud et al. 6* (P); en limite de St. Benoît et Salazie, Forêt de Bélouve, sentier du Mazerin, en bas de pente du côteau Monique, [21°2′0″S, 55°33′0″E], *E. Grangaud et al. 7* (P), *E. Grangaud et al. 8* (P); Bois à Hellbourg, [21°3′0″S, 55°32′0″E], 11 Sep. 1882, *s. coll. s.n.* (P). **St. Denis:** Bois du Boucan Launay, [20°53′0″S, 55°27′0″E], *L. H. Boivin 814* (P); Le Boucan Launay, au dessus de l'Habitation de Mr. Valentin, [20°53′0″S, 55°27′0″E], s.d., *L. H. Boivin 884* (P). **St. Paul:** Rte. forestière du Pic Maïdo, [21°4′36.53″S, 55°23′0.43″E], *F. Badré 781* (P). **St. Pierre:** Cilaos, Bonnet Carré, [21°6′0″S, 55°26′0″E], *F. Badré 914 bis* (P); Cilaos, Bonnet Carré, [21°6′0″S, 55°26′0″E], *F. Badré 914* (P); Saint Philippe, Basse Vallée, [21°20′12.44″S, 55°42′9.58″E], *F. Badré 1001* (P); Saint Philippe, Forêt de La Mare Longue, [21°22′0″S, 55°45′0″E], *F. Badré 1009* (P); Le Tampon, Forêt de Sainte Thérèse, pointe du Bras Creux, *E. Grangaud et al. 1823* (*1* and *2*) (P); betw. St. Philippe & St. Joseph, La Vallée Heureuse, above Basse Vallée, [21°19′9.30″S, 55°41′41.12″E], *K. U. Kramer, F. Gartmann & M. Kramer 9291a* (P).

3. Megalastrum lanuginosum (Willd. ex Kaulf.) Holttum, Gard. Bull. Singapore 39: 161. 1986 [1987]. Basionym: *Aspidium lanuginosum* Willd. ex Kaulf., Enum. Filic. 244. 1824. *Nephrodium lanuginosum* (Willd. ex Kaulf.) Desv., Mém. Soc. Linn. Paris 6: 262. 1827. *Lastrea lanuginosa* (Willd. ex Kaulf.) T. Moore, Index Fil. 87. 1858. *Polystichum lanuginosum* (Willd. ex Kaulf.) Keyserl., Polyp. Herb. Bunge 45. 1873. *Dryopteris lanuginosa* (Willd. ex Kaulf.) C. Chr., Index Fil. 273. 1905. *Ctenitis lanuginosa* (Willd. ex Kaulf.) Copel., Gen. Fil. 124. 1947. TYPE: Mauritius. s. loc., s.d., *L. M. A. Aubert du Petit-Thouars s.n.* (holotype, B-W 19808 [2 sheets likely representing a single specimen]!). Figures 2A–F, 3C.

Nephrodium elatum Desv., Mém. Soc. Linn. Paris 6: 262. 1827, non *Nephrodium elatum* Baker, 1874. TYPE: La Réunion. s.d., *s. coll. s.n.* (holotype, P 00610737!).

Aspidium catopteron Kunze, Linnaea 10: 550. 1836. *Lastrea catoptera* (Kunze) Pappe & Rawson, Syn. Fil. Afr. Austr. 12. 1858. *Nephrodium catopteron* (Kunze) Hook., Sp. Fil. 4: 137. 1862. *Dryopteris catoptera* (Kunze) Kuntze, Revis. Gen. Pl. 2: 812. 1891. TYPE: South Africa. Koratra, "in valle rupestri umbrosa secus rivulum inter Omsamcaba et Omsamwubo et prope Koratra in sylva 500–1000 p.," 1838, *J. F. Drège s.n.* (lectotype, designated by Roux [1986: 377], BM not seen; duplicates, NY, S).

Lastrea odorata C. Presl, Tent. Pterid. 77. 1836, nom. nud.

Aspidium odoratum Mett., Abh. Senckenberg. Naturf. Ges. 2: 399. 1858, nom. nud., non *Aspidium odoratum* Bory ex Willd., 1810.

Rhizomes massive, erect or procumbent, sometimes arborescent (resembling a small tree fern) and forming a trunk to 50(–100) cm high, 15 cm thick, scaly, the scales to 30 × 3 mm, linear, thin, translucent, light golden brown, papyraceous, subentire and irregularly dentate-serrulate toward the apex; fronds to 2.5 m; petiole bases subglabrous, rarely bearing a few scales similar to those on the rhizome, but smaller, to 4 × 0.5 mm; laminae to 1.5 m, deltate, triangular to pentagonal; blades tripinnate-pinnatifid to tripinnate-pinnatisect (rarely quadripinnate-pinnatifid) at base, bipinnate-pinnatifid or bipinnate-pinnatisect medially (rarely tripinnate-pinnatifid); basal pinnae to 100 cm, the stalks to 3.5 cm, strongly inequilateral with the basal basiscopic pinnules much more elongate, the most basal basiscopic pinnules to 35 cm, to 5 times the length of the most basal acroscopic ones, the pinnules on the acroscopic side slightly reduced toward the pinna base; pinna rachises abaxially puberulent to pubescent, eglandular, the hairs erect to spreading, 0.2–1 mm, to 8-celled, very sparsely scaly, the scales 0.5–1 × 0.2–0.3 mm, linear, entire, flat and nonbullate, dark brown to light brown, adaxially densely pubescent, the hairs erect, 0.3–1 mm long, 5- to 8-celled, septate, eglandular; costules abaxially pubescent, glandular or eglandular, the glands spherical, yellowish translucent, shiny, sessile or stalked, ca.

0.1 mm diam., 1- or 2-celled, the hairs spreading, (0.2–)0.5–1.7 mm long, 6- to 8-celled, very sparsely to abundantly scaly, the scales 0.3–1.5 × ca. 0.3(–0.5) mm, flat to conspicuously bullate, entire, light brown, dull, rarely clathrate, adaxially pubescent, eglandular, the hairs erect to spreading, 0.5–0.7(–1.2) mm, 3- to 5-celled, septate; laminar tissue between veins from pubescent on both surfaces to subglabrous on both surfaces, abaxially eglandular or sparsely glandular, the glands like those of the costules, hairs erect to spreading, 0.2–1.2 mm, 3- to 8-celled, thicker on the adaxial surfaces; veins 3 to 5 pairs per pinnule lobe, visible on both surfaces, ending at or close to (rarely before) laminar margins (except for those veins with sori that end well before laminar margins) in enlarged clavate tips as conspicuous hydathodes, abaxially pubescent and sparsely glandular to eglandular, glands spherical, yellowish clear, shiny, sessile or stalked, ca. 0.1 mm diam., hairs erect, 0.3–1 mm, usually 4- to 6-celled, adaxially pubescent, hairs erect to spreading, 0.4–0.8 mm long, 4- to 6-celled; laminar margins ciliate, hairs similar to those on laminar tissue; sori on acroscopic branches of forked veins, indusia present and persistent, covering sporangia, orbicular-reniform, to 1.5 mm diam., dark brown, shiny, densely pubescent to glabrous, densely glandular or eglandular, glands 1- or 2-celled, yellowish, shiny, hairs to 0.7 mm, margins dull and erose; spore monolete, the perispores nonfenestrate, echinulate.

Distribution and ecology. *Megalastrum lanuginosum* has a disjunct distribution between tropical West Africa, where it is restricted to Bioko and São Tomé (one specimen—not seen—is cited from Río Muni, the continental region of Equatorial Guinea; Velayos et al., 2008), and eastern Africa and the Madagascan region, the latter including tropical East Africa, eastern South Africa, Madagascar, the Mascarene Islands (La Réunion and Mauritius), and the Comoros (Fig. 1). It is rare or perhaps extinct in the Mascarene Islands (no collection since 1925, although it was recently sought in La Réunion; E. Grangaud, pers. comm.) and rare and local in the Gulf of Guinea islands (Benl, 1991), but *M. lanuginosum* can be locally common in East Africa.

This is a terrestrial fern encountered in deep shade of evergreen forests, in swampy areas, and most frequently observed near or on banks of permanent streams, from 850 to 2150 m. *Megalastrum lanuginosum* has also been present in cloud forests, and mentioned once from a rock fissure. The taxon can resemble a small tree fern, likely to 1 m high, according to the annotation on *E. A. C. L. E. Schelpe 1689* (BOL).

Etymology. The specific epithet is taken from the Latin "lanugo," meaning wool or down, referring to the pubescence of the leaves. Although this is the condition of most specimens of *Megalastrum lanuginosum*, some specimens are only sparsely pubescent.

Discussion. *Megalastrum lanuginosum* differs from the two endemic Mascarene species by the laminae at least tripinnate-pinnatifid at the base (rarely quadripinnate), appearing more finely dissected when compared to the bipinnate-pinnatifid laminae in *M. lanatum* and *M. canacae*. Other useful differentiating characters include the scales of the rhizomes that are light golden brown, papyraceous, with small irregular marginal teeth toward the apex, and the large, conspicuous, and persistent indusia. Leaf veins usually end at or close to (rarely before) the laminar margins, which is remarkable in the genus. Only the Neotropical *M. inaequale* (Kaulf. ex Link) A. R. Sm. & R. C. Moran shares this character.

Other morphological characters are extremely variable in *Megalastrum lanuginosum*. Although bullate scales are found only in *M. lanuginosum* and observable on almost all specimens, their density and size show great variation among specimens. Contrary to Holttum (1983), we found a few small bullate scales on Mascarene specimens (to see these scales, careful inspection with at least 10× magnification is required on the abaxial surfaces of costules). Because numerous morphological intermediates exist, from densely to sparsely scaly costules, and from large to small bullate scales, individual species cannot be distinguished on the basis of indument. Also, the indusia vary in the presence and abundance of hairs and glands, and in hair length. We find no other character correlating with this, and therefore we interpret these variations as phenotypic plasticity within a single taxon.

Megalastrum lanuginosum varies greatly in indument, especially as to the location, abundance, and length of hairs, and these characters overlap with those of *M. lanatum*. This variation does not correlate with geography. For example, the length of hairs on pinna rachises, costules, and veins varies even within the Mascarene Islands. Most of the specimens have long hairs (exceeding 0.5 mm), whereas two specimens (*s. coll. s.n.*, in Hb. Desvaux, La Réunion, P 00610737; *J. B. G. M. Bory de St. Vincent s.n.*, Mauritius, P 00483107 and P 00477882) have shorter hairs (less than 0.4 mm). Similarly, in Bioko, the laminar tissue between the veins is glabrous in some specimens but pubescent in others.

Additional specimens examined. COMOROS. **Grande Comore:** Massif du Karthala, versant O, piste menant de

Boboni à Convalescence, 11°45′S, 43°17″E, *F. Rakotondrainibe et al. 6727bis* (P). **Mayotte:** Forêt de Combani, [12°47′48″S, 45°9′24″E], *L. Humblot 1289* (P); 17 Oct. 1884, *L. Humblot 1323* (K, P).

EQUATORIAL GUINEA. **Bioko:** Pico, [3°35′0″N, 8°46′0″E], *G. Benl & Benl 378 FP* (P); Malabo-Pico Basile, etrada Km 12, plantacoes de cacau, [3°35′0″N, 8°46′0″E], *M. Fidalgo de Carvalho 3564* (NY); Peak, [3°35′0″N, 8°46′0″E], *G. Mann 349* (K); s. loc., [3°35′0″N, 8°46′0″E], 1861, *G. Mann s.n.* (K).

KENYA. **Embu Distr.:** Mt. Kenya SE, Irangi Forest Station, 0°21′S, 37°27′E, *R. B. Faden et al. 72/190* (BOL, K, MO). **Kiambu Distr.:** Kikuyu Escarpment Forest (S. Aberdare Forest), Karamenu River Valley adjacent to Sasumua pipeline & Karamenu Rivers, 0°51′37″S, 36°45′15″E, *R. B. Faden et al. 71/282* (BOL). **Meru Distr.:** Ithagune forest, rd. along base of volcanic cone Kirue, 9 mi. from Nkubu, [0°4′0″S, 37°40′0″E], *R. B. Faden et al. 69/763* (BOL, K). **Taita Distr.:** Taita Hills, Mbololo Hill, Mraru ridge, [3°21′0″S, 38°27′0″E], *R. B. Faden et al. 69/842* (BOL, K). **Taita-Taveta Distr.:** Ngangao Forest, [3°22′0″S, 38°20′0″E], *R. B. Faden et al. T468* (K); Dundori ravine, 0°12′0″S, 36°16′0″E, *R. R. Schippers 49* (WAG); Taita Hills, Ngangoa Forest, 3°25′0″S, 38°20′0″E, *R. R. Schippers 249* (WAG). **Thika Distr.:** Kieni Forest, S side, 0°51′0″S, 36°40′0″E, *R. R. Schippers 548* (WAG).

LA RÉUNION. s. loc., 1925, *G. Carles s.n.* (P); s. loc., s.d., *s. coll. s.n.* (P); s. loc., s.d., *s. coll. s.n.*, (P-Desvaux).

MADAGASCAR. **Antananarivo:** Tsinjoarivo, Forêt d'Ankilahila à 19.2 km au SE de Tsinjoarivo, le long de la rivière d'Andrindimbolo, 19°42′24″S, 47°50′6″E, *G. Borie 554* (P, TEF); Ankazobe, Manankazo, Réserve spec. d'Ambohitantely, ca. 8 km au NO d'Ankazobe, 18°10′S, 47°17′E, *F. Rakotondrainibe 419* (P, TEF); Anjozorobe, Forêt d'Andranomay, 2 km au NNE d'Andranomay, 13 km au SE d'Anjozorobe, 18°28′48″S, 47°57′18″E, *F. Rakotondrainibe 3720* (MO, P); Ankazobe/Manankazo, RS d'Ambohitantely, partie méridionale de la réserve, 18°13′S, 47°17′E, *F. Rakotondrainibe & Randriambololona 4461* (P). **Antsiranana:** Andapa, Befingotra, RS d'Anjanaharibe-Sud, sur le versant SE, à 6.5 km au SSO de Befingotra, 14°45′18″S, 49°30′18″E, *F. Rakotondrainibe & Raharimalala 2194* (P, TEF). **Fianarantsoa:** Ambalavao, Ambatomboay, RNI d'Andringitra versant Est, 40 km S d'Ambalavao, sur les berges d'un affluent de la rivière Sahavatoy, 22°13′22″S, 46°58′18″E, *F. Rakotondrainibe 2695* (P, TEF); Ambalavao, RS d'Ivohibe, à 8 km à l'Est du village d'Ivohibe, 22°29′0″S, 46°58′6″E, *F. Rakotondrainibe & Randriambololona 4176* (P); Ranomafana-Ifanadiana, PN de Ranomafana, forêt de Vatoharanana, à 4 km au SO du village de Ranomafana, 21°17′24″S, 47°26′00″E, *F. Rakotondrainibe & Randriambololona 5919* (P). **Mahajanga:** Forêt du Bangolava, 120 km O de Tsiromandioly vers Morafenobe, [16°5′0″S, 47°18′0″E], *G. Cremers 3268* (P); near Andribe, forest remnant at high plateau, 17°30′S, 47°0′E, 1500 m, *H. van der Werff & McPherson 13545* (MO, UC). **Toamasina:** Ambatondrazaka, Ankaroka, [19°7′0″S, 44°44′0″E], *G. M. Cours 209* (P); Moramanga, Forêt de Sandrangato, au S de Moramanga, [19°10′0″S, 48°15′0″E], *R. Decary 17837* (P); Grande forêt d'Analamazoatra, [18°56′0″S, 48°25′0″E], *C. Alleizette 19* (P); Mandraka, [18°55′0″S, 47°56′0″E], *C. Alleizette 77* (P), *C. Alleizette 171* (P), *C. Alleizette 182* (P); Andovoranto, Moramanga, forêt d'Analamazotra [18°56′0″S, 48°25′0″E], *R. Viguier & Humbert 869* (P). **Toliara:** Massif du Kalambatitra, Mt. Kalambatritra et ses abords, [23°22′0″S, 46°29′0″E], *H. Humbert 11905* (P); Massif du Kalambatritra, Mt. Analatsitendrika, [23°22′0″S, 46°29′0″E], *H. Humbert 11944* (P, TAN); Tolanaro, Eminiminy, parcelle 1, RNI n°11 d'Andohahela, versant E et sommet du Trafon'omby, 13.5 km au NW d'Eminiminy, Camp 3, 24°35′4″S, 46°44′8″E, *F. Rakotondrainibe 3080* (P); Tolanaro, Eminiminy, parcelle 1, RNI n°11 d'Andohahela, versant E et sommet du Trafon'omby, Camp 4, 15 km au NW du village d'Eminiminy, [24°33′0″S, 46°43′0″E], *F. Rakotondrainibe 3128* (P); Fivondronana, Betroka, Ivahona, Voromiantsa, forêt dense de Befarafara, Kalambatritra, 23°25′2″S, 46°27′5″E, *R. Razakamalala et al. 1992* (P).

MALAWI. **Kota-Kota Distr.:** Nchisi Mtn., [13°19′0″S, 34°3′0″E], *L. J. Brass 17040* (K, MO, NY, US); Cholo Mtn., [16°5′0″S, 35°3′0″E], *L. J. Brass 17757* (K, MO, NY, US); Nchisi forest, [13°19′0″S, 34°3′0″E], *J. D. Chapman 836* (BOL). **Thyolo Distr.:** Mt. Thyolo, [16°10′0″S, 35°10′0″E], *J. P. Roux 2916* (NBG).

MAURITIUS. Escalier woods, s.d., *H. Barkly s.n.* (K); des grands bois du Milieu, [20°17′12″S, 57°35′3″E], Oct. 1801, *J. B. G. M. Bory de St Vincent s.n.* (P); s. loc., 1871, *W. Cattell s.n.* (NY); s. loc., *s. coll. 72* (P); s. loc., *F. W. Sieber 48* (BR, K, MO, P, S); s. loc. [possibly from Mauritius], s.d., *L. M. A. Thouars s.n.* (P).

MOZAMBIQUE. Bandula Mtns., [19°0′42″S, 33°8′36″E], *N. C. Chase 6596* (BOL, K). **Manica/Sofala:** Yaegersberg, Gavuso, [19°4′32″S, 33°55′34″E], *E. A. C. L. E. Schelpe 5621* (BOL, NBG). **Zambezia Prov.:** Namuli, Makua country, [15°22′27″S, 37°2′26″E], s.d., *J. T. Last s.n.* (K); Morrumbala, [16°59′0″S, 35°38′0″E], *E. P. Luja 347* (BR); Morrumbala, [16°59′0″S, 35°38′0″E], *E. P. Luja 348* (BR, P).

SÃO TOMÉ ISLAND. s. loc., [0°16′0″N, 6°33′0″E], 1861, *G. Mann s.n.* (K).

SOUTH AFRICA. In valle rupestris umbrosa secus rivulum inter Omsamcaba et Omsamwubo et prope Koratra in sylva, 1844, *J. Drège s.n.* (NY); Westfalia state, s. loc., *J. C. Scheepers 436* (PRE); s. loc., s.d., *D. Brown s.n.* (BOL); s. loc., s.d., *J. Drège s.n.* (K). **Eastern Cape:** Transkei, Tsolo, Ntywenka, [30°44′0″S, 28°45′0″E], *S. Cawe 735* (BOL); Transkei, Port St. Johns, [31°36′21″S, 29°31′11″E], *A. G. M. McLoughlin 785D* (BOL). **Kwazulu-Natal:** s. loc., [29°0′0″S, 30°0′0″E], *Beivsher? 3/88* (US) [29°0′0″S, 30°0′0″E], *J. Buchanan 138* (NY); s. loc., [29°0′0″S, 30°0′0″E], *J. Buchanan 558* (US); s. loc., [29°0′0″S, 30°0′0″E], *J. Buchanan 559* (US); Lions River, Dargle, [29°29′0″S, 30°10′0″E], *E. Esterhuysen 26199* (BOL, US); Mowbray' Ahrens, [29°4′0″S, 30°46′0″E], *B. S. Fisher 947* (BOL); s. loc., [29°0′0″S, 30°0′0″E], s.d., *R. J. Garden s.n.* (K); s. loc., [29°0′0″S, 30°0′0″E], *W. T. Gerrard 1933* (K); s. loc., [29°0′0″S, 30°0′0″E], *W. T. Gerrard 1953* (GH); s. loc., [29°0′0″S, 30°0′0″E], *M. J. M. Ken 52* (K); S Natal, Weza State Forest, Mpetsheni Forest, [30°36′0″S, 29°40′0″E], *A. Nicholas & Marais 1674* (MO, PRE); Natal, Dlinza Forest Res., Eshowe, [28°53′18″S, 31°26′54″E], *B. S. Parris & Croxall 7273* (K), *B. S. Parris & Croxall 7276* (K); Lidgetton, [29°27′0″S, 30°6′0″E], *A. Roberts 970c* (PRE); Khandla forest, Zululand, [28°0′0″S, 32°0′0″E], *E. A. C. L. E. Schelpe 1689* (BOL); Ngotsche, Ngome forest, [27°52′0″S, 31°24′0″E], *E. A. C. L. E. Schelpe 6220* (BOL, US); Kranskop, [28°28′0″S, 29°22′0″E], 13 Apr. 1980, *E. J. van Jaarsveld 2830* (NBG); 10 km from Kwasizabantu toward Mapumulo, S slope, [29°11′0″S, 31°3′0″E], *E. J. van Jaarsveld 5104* (K, MO, PRE, S); Kranskop, [28°55′0″S, 30°57′0″E], *E. J. van Jaarsveld 5116* (PRE); s. loc., [29°0′0″S, 30°0′0″E], s.d., *Wood? s.n.* (US); Inanda,

[29°37′0″S, 30°56′0″E], s.d., *M. Wood s.n.* (MICH, UC). **Limpopo:** Transvaal, Magoebaskloof, [23°51′0″S, 30°01′0″E], *N. C. Anthony 2330* (NBG); Transvaal, Broederstroom & Woodl. Reserve, [23°46′0″S, 30°1′0″E], *A. F. Braithwaite 258* (BOL); NE Transvaal, Grootbos', woodbush Forest Res., Tzaneen, [23°49′0″S, 30°10′0″E], *J. E. Burrows 3244* (BOL); Transvaal, Pilgrim Rest distr., Mount Sheba Nature Res., [24°56′0″S, 30°43′0″E], *J. Jacobsen 4432* (PRE); Transvaal, Mac Mac Natuurreservaat, [24°59′0″S, 30°50′0″E], *J. P. Kluge 2257* (PRE); New Agatha Forest Res., [24°01′0″S, 30°04′0″E], *P. J. Muller & J. C. Scheepers 101* (WAC); Transvaal, Houtbosch, [24°51′0″S, 30°57′0″E], *A. Rehmann 5601* (K); Woodbush Forest Res., [23°46′0″S, 30°4′0″E], *J. P. Roux 2330* (NBG); Transvaal, Entabeni, Zoutpansberg, [22°58′0″S, 29°45′0″E], *E. A. C. L. E. Schelpe 6011* (BOL, US); Transvaal, Entabeni, [22°58′0″S, 29°45′0″E], *L. E. Taylor 754* (NY, UC). **Western Cape:** Cape, [33°58′0″S, 18°25′0″E], s.d., *J. Bowie s.n.* (K); Austral Africa, *W. J. Burchell 5436* (GH, K, NY, S); ca. 1 km W of Bloukrans River Bridge, Bloukrans Pass, [33°58′02.17″S, 23°38′42.62″E], *J. E. Burrows 1453* (BOL, NBG); Cape, [33°58′0″S, 18°25′0″E], *s. coll. 775* (GH); s. loc., s.d., *s. coll. s.n.* (NY); Cape, Lusikisiki, Egoso forest above Magwa waterfall, [31°26′0″S, 29°38′0″E], *Venter & Vorster 81* (MO, PRE, US).

TANZANIA. **Iringa:** Ludewa Distr., forests around Milo village, [9°53′0″S, 34°39′0″E], *J. Lovett et al. 13685* (AAU). **Morogoro:** Uluguru Mtns., Mwere valley, [7°10′0″S, 37°40′0″E], *R. B. Faden et al. 70/585* (K); N. Uluguru Forest Res., Lupanga Peak, E side, [6°52′0″S, 37°43′0″E], 1991, *J. B. Hall s.n.* (K); Kanga Mtn., N Nguru, 6°0′S, 37°43′E, *J. Lovett & D. W. Thomas 2791* (MO); Kilombero Distr., Mwanihana Forest Res. above Sanje village, 7°50′S, 36°55′E, *D. W. Thomas 3862* (MO, P). **Tanga:** Lushoto Distr., Shume-Magamba Forest Res., [4°40′0″S, 38°15′0″E], *C. M. Kisena 459* (K).

ZIMBABWE. s. loc., s.d., *J. Drège s.n.* (MO). **Melsetter Distr. [Chimanimani]:** [19°53′0″S, 32°49′0″E], *N. C. Chase 4833* (MO, PRE); Muchira River, S of Mont Peni, [19°59′0″S, 32°54′0″E], *B. Goldsmith 27/73* (BOL, MO, P); Gungunyana Forest, [20°24′0″S, 32°43′0″E], *A. J. Whellan 219* (NY). **Mutare Distr.:** Vumba Mtns. Distr., stream on S slopes of Bungo forest, [19°5′0″S, 32°45′0″E], *J. E. Burrows 1678* (BOL); Umtali Distr., Vumba, [19°5′0″S, 32°45′0″E], *N. C. Chase 5140* (GH, MO, NBR, PRE, S, UC), *N. C. Chase 5703* (BOL); Vumba Mtns. Distr., s. loc., [19°5′0″S, 32°45′0″E], *E. A. C. L. E. Schelpe 5375* (BOL, MO, P, PRE).

Excluded Species

The following taxa have been previously ascribed to *Megalastrum*. However, they do not have the characteristic of the venation and cutting of *Megalastrum*: the basal basiscopic vein on the distal pinnules arises from the costules (not from the costa, as in *Megalastrum*). Furthermore, hairs present on the adaxial surfaces of the axes differ from those of *Megalastrum* in having cells apparently twisted relative to each other when dried. Finally, the following taxa have unicellular, cylindrical, glandular hairs on the stalks of the sporangia. All these morphological characters define the following taxa as belonging in *Ctenitis*.

Ctenitis exaggerata (Baker) Ching, Sunyatsenia 5: 250. 1940. Basionym: *Nephrodium crinitum* (Poir.) Desv. var. *exaggeratum* Baker, Ann. Bot. (Oxford) 5: 319. 1892. *Dryopteris exaggerata* (Baker) C. Chr., Dansk Bot. Ark. 7: 60, t. 16, f. 4–7. 1932. *Megalastrum exaggeratum* (Baker) Holttum, Gard. Bull. Singapore 39: 161. 1986 [1987]. TYPE: Madagascar. Antananarivo, s.d., *W. Pool s.n.* (holotype, K 000351137!).

Ctenitis magna (Baker) Tardieu, in Humbert, Fl. Madagasc. 5: 344. 1958. Basionym: *Nephrodium magnum* Baker, J. Bot. 22: 142. 1884. *Dryopteris magna* (Baker) C. Chr., Index Fil. 276. 1905. *Megalastrum magnum* (Baker) Holttum, Gard. Bull. Singapore 39: 161. 1986 [1987]. TYPE: Madagascar. s.d., *L. Humblot 265* (holotype, K 000351140!; isotypes, K 000351141!, P 00483091!, P 00483092!, P 00483093!, P 00610798!).

Polypodium baronii Baker, J. Linn. Soc., Bot. 22: 535. 1887, as "*baroni.*" *Dryopteris baronii* (Baker) C. Chr., Index Fil. 254. 1905. TYPE: Madagascar. s.d., *R. Baron 3920* (holotype, K 000351138!, K 000351139!).

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APPENDIX 1. Index to collections. Each specimen is cited by the first collector, listed alphabetically by the first author's last name. The numbers in parentheses refer to the accepted species number in the taxonomic treatment.

Alleizette, C. 19, 77, 171, 182 (3); *Anthony, N. C. 2330* (3).

Badré, F. 781, 914, 914bis, 1001, 1009, 1052 (2); *Beivsher? 3/88* (3); *Benl, G. 378 FP* (3); *Bernier, C. 92* (2); *Boivin, L. H. 122, 814, 884* (2); *Borie, G. 554* (3); *Braithwaite, A. F. 258* (3); *Brass, L. J. 17040, 17757* (3); *Buchanan, J. 138, 558, 559* (3); *Burchell, W. J. 5436* (3); *Burrows, J. E. 1453, 1678, 3244* (3).

Cadet, T. 4345 (2); *Cawe, S. 735* (3); *Chapman, J. D. 836* (3); *Chase, N. C. 4833, 5140, 5703, 6596* (3); *Cours, M. G. 209* (3); *Cremers, G. 3268* (3).

De L'Isle, M. G. 429 (2); *Decary, R. 17837* (3).

Esterhuysen, E. 26199 (3).

Faden, R. B. 69/763, 69/842, 70/585, 71/282, 72/190, T468 (3); *Fidalgo de Carvalho, M. 3564* (3); *Fisher, B. S. 947* (3).

Gerrard, W. T. 1933, 1953 (3); *Goldsmith, B. 27/73* (3); *Grangaud, E. 1243bis, 1547, 1824, 4, 5* (1); *6, 7, 8, 1823–1, 1823–2* (2).

Humbert, H. 11905, 11944 (3); *Humblot, L. 1289, 1323* (3).

Jacobsen, J. 4432 (3).

Ken, M. J. M. 52 (3); *Kisena, C. M. 459* (3); *Kluge, J. P. 2257* (3); *Kramer, K. U. 9291a* (2).

Lovett, J. 2791, 13685 (3); *Luja, E. P. 347, 348* (3).

McLoughlin, A. G. M. 785D (3); *Muller, P. J. 101* (3).

Nicholas, A. 1674 (3).

Parris, B. S. 7273, 7276 (3).

Rakotondrainibe, F. 419, 2194, 2695, 3080, 3128, 3720, 4176, 4461, 5919, 6727bis (3); *Razakamalala, R. 1992* (3); *Rehmann, A. 5601* (3); *Richard, J. M. C. 46* (2); *Roberts, A. 970c* (3); *Roux, J. P. 2330, 2916, 3414* (3).

Scheepers, J. C. 436 (3); *Schelpe, E. A. C. L. E. 1689, 5375, 5621, 6011, 6220* (3); *Schippers, R. R. 49, 249, 548* (3); *Sieber, F. W. 36* (1), *48* (3); *Strahm, W. 20906* (1).

Taylor, L. E. 754 (3); *Thomas, D. W. 3862* (3).

van der Werff, H. 13545 (3); *van Jaarsveld, E. J. 2830, 5104, 5116* (3); *Venter 81* (3); *Viguier, R. 869* (3).

Whellan, A. J. 219 (3).

POLLINATION SYNDROMES OF NEW WORLD *SALVIA* SPECIES WITH SPECIAL REFERENCE TO BIRD POLLINATION[1]

Petra Wester[2,3,4] *and Regine Claßen-Bockhoff*[2]

Abstract

The genus *Salvia* L. (Lamiaceae) encompasses about 1000 species, approximately two thirds of which are in the New World. Bees and birds are known as pollinators, but a more detailed analysis of the pollinator groups is lacking. This paper presents a complete list of all currently accepted New World *Salvia* species and their classification according to their pollination syndromes, focusing particularly on bird-pollinated species. The concept of pollination syndromes is used and complemented by field investigations, morphometric measurements, and experiments to reconstruct the process of pollen transfer and to confirm the fitting or exclusion of a given pollinator group. Within the 602 New World *Salvia* species, 58% are identified to be melittophilous (bee pollinated) and 31% to be ornithophilous (bird pollinated). *Salvia whitehousei* Alziar is assumed to be psychophilous (butterfly pollinated/long-tongued fly pollinated). About 11% of the species show characters of two or more syndromes and eight species are not assignable to any group. Bird-pollinated *Salvia* species occur from North America southward to Chile and Argentina. They usually grow as shrubs or perennial herbs (97%) and have red flowers (at least 49%) of an average size of 34 mm (7–130 mm). With respect to their floral diversity and phylogeny, parallel evolution is evident.

Resumen

El género *Salvia* L. (Lamiaceae) comprende unas 1000 especies, de las cuales aproximadamente dos tercios habitan en el Nuevo Mundo. Abejas y aves han sido descritas como polinizadores en este clado, sin embargo, hasta ahora no se han realizado estudios detallados acerca de los grupos de polinizadores involucrados. El presente trabajo entrega un registro completo de las especies de *Salvia* del Nuevo Mundo actualmente aceptadas y su clasificación de acuerdo a los síndromes de polinización, con énfasis en las especies polinizadas por aves. De las 602 especies de *Salvia* del Nuevo Mundo, 58% se identifican como melitófilas (polinizadas por abejas) y 31% como ornitófilas (polinizadas por aves). Sólo *S. whitehousei* Alziar es considerada como psycófila (polinizada por mariposas/moscas de larga probóscide). Cerca del 11% de las especies presenta caracteres de dos

[1] We thank many people for helping us with plant material, access to herbarium specimens (AAU, ARIZ, B, BIGU, BM, C, CGE, COL, COLO, F, FLAS, G, GH, GOET, H, HAO, HUT, K, L, LD, LPB, MEXU, MICH, MJG, MO, NA, NY, OAX, P, RSA, S, SD, TEX-LL, UC-JEPS, UCR, US, W, WU, XAL, and ZEA) and bird skins, identification of sages and birds, logistic support, permits for research and collection, information and stimulating discussions, taking care of the plants in the Botanischer Garten Mainz, proofreading a draft of the paper, and refining our illustrations. We are especially grateful to W. Anderson (Chihuahuan Desert Gardens, El Paso, Texas, U.S.A.), H. Bahmann and F. Hoppe (Botanischer Garten Mainz, Germany), C. Barnhill (Fullerton Arboretum, Fullerton, California, U.S.A.), S. Beck and R. I. Meneses (LPB), A. and F. Berndt (Cochabamba, Bolivia), C. Cahill (New York), G. Castillo (XAL), C. Cházaro and F. Gómez (Xalapa, Mexico), M. Cházaro (Universidad de Guadalajara, Mexico), O. Clarke and M. Alexander (Riverside, U.S.A.), B. Clebsch (La Honda, U.S.A.), M. Dimmitt (Arizona-Sonora Desert Museum, Tucson, Arizona, U.S.A.), A. Espejo and A. R. López (UAMIZ), H. Forbes (University of California Botanical Garden at Berkeley, U.S.A.), D. Franke and L. Klöckner (Johannes Gutenberg-Universität Mainz), C. Froissart (Olivet, France), M. García (MEXU), C. González and J. F. Ornelas (Instituto de Ecología, Xalapa, Mexico), E. Groot (Albert-Ludwigs-Universität Freiburg, Germany), J. Henrickson and T. Wendt (TEX), I. Kaczmarek (Botanischer Garten Hamburg, Germany), M. Kraemer (Universität Bielefeld, Germany), J. Luna (Tequila, Mexico), N. Martínez and R. Martínez (HEM), R. Middleton (Surrey, U.K.), B. O'Brien and T. Thibault (Rancho Santa Ana Botanic Garden, Claremont, California, U.S.A.), H. Oliva and F. Ramón (CORU), M. Ordano (UNAM, Mexico), C. Quiroga (Colección Boliviana de Fauna, La Paz, Bolivia), O. Reyna (Universidad de Guadalajara, Mexico), A. Sanders, M. Provance, and T. Salvato (UCR), A. Saynes (Sociedad para el Estudio de los Recursos Bióticos de Oaxaca [SERBO]), M. Sazima (Universidade Estadual de Campinas, Brazil), A. Schmidt-Lebuhn (Centre for Australian National Biodiversity Research, Canberra, Australia), G. Stiles (Universidad Nacional de Colombia, Bogotá, Colombia), U. Urban (Rodenberg, Germany), A. M. van Nest (Austin, Texas, U.S.A.), A. Vázquez (IBUG), M. Véliz (BIGU), H. Vibrans (CHAPA), S. Vogel (Universität Wien, Austria), J. B. Walker (University of Wisconsin-Madison, U.S.A.) and R. Walker (San Diego, California, U.S.A.), A. Weller and K.-L. Schuchmann (Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany), C. Westerkamp (Universidade Federal do Ceará, Crato, Brazil), M. Wetherwax (JEPS), J. Wood (OXF), and R. Worthington (UTEP). The Deutsche Forschungsgemeinschaft (DFG Cl 81/9–1) and the Feldbausch-Stiftung (Mainz) are gratefully acknowledged for financial support.

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o más síndromes distintos y ocho especies no son asignables en ningún grupo. Especies de *Salvia* polinizadas por aves se encuentran desde Norteamérica hasta Chile y Argentina por el sur. Éstas adoptan generalmente una forma de vida arbustiva o de herbáceas perennes (97%) y evidencian flores rojas (al menos 49%) con un tamaño promedio de 34 mm (7–130 mm). Acorde a la filogenia, la diversidad floral observada evidencia evolución en paralelo dentro del género.

Key words: Floral morphology, Lamiaceae, melittophily, morphometry, New World *Salvia* species, ornithophily, parallel evolution, pollination syndrome, pollinator fitting and exclusion, psychophily.

Historically, the genus *Salvia* L. (sages, ca. 1000 species; Lamiaceae) has been associated with European bee-pollinated species, e.g., *S. pratensis* L. and *S. officinalis* L. With these species, Sprengel (1793) observed pollen transfer by the genus-specific staminal lever mechanism for the first time (see Claßen-Bockhoff et al., 2003). Today, this Europe- and bee-centered view is inadequate because two thirds of all *Salvia* species occur in the New World, many of them being bird pollinated (Alziar, 1988b, 1989a, 1989b, 1990, 1992, 1993; Wester & Claßen-Bockhoff, 2007).

Nevertheless, bees are the dominant pollinator group in the genus (e.g., Hildebrand, 1865; Grant & Grant, 1964; Kugler, 1972; Hedström, 1985; Dieringer et al., 1991; Claßen-Bockhoff et al., 2004b). Only rarely were other insects like butterflies, moths, or flies observed or assumed to be pollinators (Sprengel, 1793; Hildebrand, 1865; Müller in Möller, 1921; Faegri & van der Pijl, 1971; Read, 1983; Grases & Ramírez, 1998; Potgieter & Edwards, 2001; Fenster et al., 2004; Wester & Claßen-Bockhoff, 2006a, 2006b; Wester, unpublished). Except for four Old World species (Wester & Claßen-Bockhoff, 2006b), bird-pollinated flowers are restricted to the New World (Delpino, 1868–1874; Trelease, 1881; Cruden et al., 1983; Reisfield, 1987; Ramamoorthy & Elliott, 1998), where hummingbirds (Trochilidae) are by far the most important flower visitors (e.g., Salvin, 1860; Wagner, 1946; Grant & Grant, 1968; Wester & Claßen-Bockhoff, 2006a; but see Torke, 2000, for the Bananaquit *Coereba flaveola* L., a passerine bird).

Although bird-pollinated flowers in *Salvia* have been known for more than 150 years (Sclater, 1856), a comprehensive study is still lacking (but see Wester & Claßen-Bockhoff, 2007). Indeed, it is completely unknown how many species are ornithophilous and whether bird pollination evolved only once or several times in parallel.

The aim of this paper is to present a survey of the bird-pollinated sages of the New World, their number, distribution, and floral diversity. In view of the ca. 600 New World species, this is an ambitious project and some methodic compromises are necessary. We combine data from our field investigations with morphometric data from herbarium specimens and the literature and postulate that specialized bird-pollinated species should have floral traits to exclude bees from reaching the nectar.

Floral traits characterizing adaptation to a certain pollinator guild are summarized in the well-known pollination syndromes (Blumenstile: Vogel, 1954) or flower classes (van der Pijl, 1961). Although they have been criticized recently (Ollerton, 1996; Waser et al., 1996; Ollerton et al., 2009), specific combinations of floral traits are helpful tools to roughly assign flowers to pollinators (see also Consiglio & Bourne, 2001; Hargreaves et al., 2004; Martén-Rodríguez et al., 2009; Wester et al., 2009). They provide, however, only a first hypothesis to be verified by field observations. Because it is impossible to study all New World sages in the field, we introduce a new test to verify the pollination syndrome. Instead of only confirming the fitting between flower and pollinator we also test the opposite, i.e., the capacity to exclude non-pollinators.

Based on all data available, we preliminarily group the New World sages as being either adapted to only one pollinator group (bees, birds, butterflies/long-tongued flies) or adapted to more than one pollinator group due to intermediate floral traits. We list all New World *Salvia* species according to their actual taxonomic status, classify the species as to their pollination syndrome, and illustrate in particular the floral diversity in bird-pollinated species.

Materials and Methods

Salvia species

In the present study 602 *Salvia* species are included. The data derive from observations of wild and cultivated plants and are supplemented by data from herbarium specimens and the literature.

Living plants were examined for 116 species. During field studies in Bolivia (February–April 2002), Mexico and Guatemala (October–December 2003), and the United States (April–June 2004), 69 species were observed in their natural habitats.

Cultivated plants (83 species) were examined at the following places: (1) the Botanical Gardens Mainz (mainly wild collections; Germany), Hamburg (Germany), University of California Botanical Garden at Berkeley, Fullerton Arboretum, Rancho Santa Ana Botanic Garden, Univerity of California Riverside Botanical Gardens, The Huntington Botanical Gardens, Tilden Regional Park Botanic Garden (all California, U.S.A.), Chihuahuan Desert Gardens (El Paso, Texas, U.S.A.); (2) the nurseries E. Hügin (Freiburg, Germany) and Native by Native Landscapes (Johnson City, Texas, U.S.A.); and (3) the private gardens of F. Berndt (Cochabamba, Bolivia), B. Clebsch (Santa Cruz, California, U.S.A.), and M. Dimmitt (Tucson, Arizona, U.S.A.).

Fresh flowers were fixed in 70% ethanol for further investigations. Vouchers are deposited at MJG with some duplicates in B, BIGU, UC-JEPS, K, LPB, MEXU, TEX-LL, and UCR (Appendix 1). Herbarium specimens originated from AAU, ARIZ, B, BIGU, BM, C, CGE, COL, COLO, F, FLAS, G, GH, GOET, H, HAO, HUT, K, L, LD, LPB, MEXU, MICH, MJG, MO, NA, NY, OAX, P, RSA, S, SD, TEX-LL, UC-JEPS, UCR, US, W, WU, XAL, and ZEA (see Appendix 1). Specimens examined in the field or herbarium specimens were identified by means of the literature (see Appendix 1), type material, and with the aid of J. Wood (OXF), A. Vázquez (IBUG), A. Espejo (UAMIZ), H. Vibrans (CHAPA), M. Véliz (BIGU), C. Froissart (Olivet, France), and A. Sanders (UCR). Because there is no actual revision of *Salvia* subg. *Calosphace* (Benth.) Benth., we did not include species with an unclear taxonomic status (partly listed as nomen dubium by Epling, 1939, or not listed in the floras), undescribed species (e.g., species ined., or sp. A in Pool, 2007), and probable hybrids from cultivation (*S. ianthina* Otto & Dietr.).

POLLINATOR OBSERVATIONS

Observations of floral visitors including birds, bees, butterflies, hawkmoths, and flies were made in the field, botanical gardens (Berkeley, Rancho Santa Ana, Riverside, and Fullerton Arboretum), and a private garden (F. Berndt, Bolivia; see also Wester & Claßen-Bockhoff, 2006a, 2007). The birds were determined after Schuchmann (1999) and with the help of J. F. Ornelas and C. González (both from Instituto de Ecología, Xalapa, Mexico), M. Ordano (Universidad Nacional Autónoma de México, Mexico City, Mexico), O. Reyna (Universidad de Guadalajara, Mexico), and G. Stiles (Universidad Nacional de Colombia, Bogotá, Colombia).

POLLEN TRANSFER SIMULATION

To test the fit between flowers and pollinators and confirm the exclusion of certain visitors as pollinators, the process of pollen transfer was experimentally simulated. For this purpose, a museum skin or metal rod was inserted into the fresh flowers (see Wester & Claßen-Bockhoff, 2006a, 2006b). The functionality of the lever mechanism, the morphometric needs for a successful pollen transfer, and the site and precision of pollen deposition were recorded at the living material. The skins were borrowed from the Colección Boliviana de Fauna, La Paz, Bolivia (CBF), and the Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany (ZFMK).

PLANT TRAITS

To identify the pollination syndrome, floral structures were morphologically and morphometrically investigated:

The length of the flower was measured from the proximal end of the flower to the distal end of the upper lip, the length of the flower tube from the proximal end of the flower to the flower entrance, and the upper lip from its distal end to the flower entrance.

Because the position of the lower lip is important for excluding bees, it was classified as reflexed (bent downward more than 90°), deflexed (bent downward about 90°), or antrorse (bent downward less than 90° to 0°). It was noted when the lips are oriented close to each other (lengthening the tube) and when the lateral lobes of the lower lip were vertically, rather than horizontally, oriented. The lower lip was called cup-shaped when its apical margins were incurved.

Flower shape was classified as bilabiate when the lips were dominant compared to the tube and tubular when the tube (with or without elongation by the lips) was more dominant. Flowers with a combination of both shape characters were classified as intermediate. Stielteller flowers (sensu Vogel, 1954) have long, slender tubes with lobes spreading at a right angle (salverform).

Structures for nectar retention at the base of the flower were classified as definite constrictions (emarginations, folds) of the corolla, definite (papillae) or weak (ridges) outgrowths of the corolla wall and hairs, and posterior lever arms (part of the staminal connectives reaching the proximal part of the flower).

Thecae exsertion indicates the distance between the distal end of the upper lip to the distal end of the thecae.

The corolla color of fresh flowers was determined after the CMYK color chart (C: cyan, M: magenta, Y: yellow, K [here S]: black; Küppers, 1999). Color data from the literature are often not well defined. We therefore classified color descriptions as follows: red includes all colorations from scarlet, claret, roseate to orange-red; pink includes rose and magenta; purple includes crimson; lavender includes light violet; blue includes royal blue; and dark violet includes almost black. If more than one color is mentioned, the species is defined in different ways or has color morphs. If known, the most frequent color was used. In a second step the colors were grouped: (a) yellow and orange; (b) red, orange, and yellow; (c) red; (d) red, purple, and pink; (e) purple, pink, and lavender; (f) blue and dark violet; and (g) white. Flowers that were not assignable to these classes because they include combinations with brownish ochre, red-brown, violet, or pale violet were grouped separately.

Floral nectar was measured as standing crop from cultivated plants (Botanischer Garten Mainz), usually in the morning of the first day of anthesis. Sugar concentration was determined using handheld refractometers (N1 [Atago, Tokyo, Japan]: 0%–32% sucrose percentage by weight [w/w]; N2 [Atago]: 28%–62% sucrose w/w; Eclipse 45–81 [Bellingham & Stanley, Kent, U.K.]: 0%–50% sucrose w/w). The volume of nectar was measured with a 25-µl microsyringe (ILS, Stützerbach, Germany).

Data on distribution, altitude, habitat, and growth forms were based mainly on the literature (see Appendix 1) and completed by our own observations. Because the growth form concept is only partly adequate for (sub-)tropical plants, we only roughly classified the species, mentioning more than one growth form when needed.

CLASSIFICATION

Pollinator groups were inferred from visitor observations; floral traits including size, shape, color, nectar, and scent; the fitting between flower and pollinator; and the capacity of the flower to exclude nonpollinator groups. We defined the exclusion of bees from the nectar by long and/or narrow corolla tubes, the exclusion of bees and butterflies by lacking landing platforms, and the exclusion of birds by very slender corolla tubes. Visitors are not pollinators if they do not touch the reproductive organs, e.g., if the stigma or pollen sacs are too far exserted to be touched by a bee. We are aware that during different seasons and at different localities the range of pollinators may vary, but nevertheless only animals that fit to the flower can act as pollinators.

RESULTS

Within the 602 examined New World sages, four groups can be distinguished. (1) Species with flowers that definitely exclude insects, but fit to birds. These are termed ornithophilous and are found in 184 species (30.6%). (2) Flowers that definitely allow bees access to nectar and morphologically fit to them. They form the largest group with 351 species (58.3%) and are grouped as melittophilous. (3) Species with flowers that exclude bees but enable butterflies or long-tongued flies to reach the nectar and touch the reproductive organs. This group only includes one species that is assumed to be psychophilous. (4) The remaining species (10.9%) do not fit to one of these groups. They are either so variable that they allow several pollinator guilds access to nectar or are not sufficiently known to be grouped (see Appendix 2).

ORNITHOPHILOUS SPECIES

In 17 species, hummingbirds were observed to pollinate the flowers, i.e., to touch pollen sacs and stigmas, while bees and butterflies were also attracted but did not pollinate. Based on these data, we identify them as ornithophilous.

They share the following (floral) traits (Table 1A, B):

Total flower length/corolla tube length. The total flower length ranges from 13 cm in *Salvia dombeyi* Epling (Fig. 1A) to 7 mm in *S. confertiflora* Pohl (Fig. 1D), and the length of the corolla tube ranges from 9 cm to 5 mm in these species, respectively (Figs. 2, 3). Regarding the geographic distribution, the longest flowers occur in the Andes (especially Peru, *S. dombeyi*), in Brazil (also where the shortest flowers occur), and in Mexico and Honduras.

Flower shape. The flower shape is bilabiate in 33 species (18%; Fig. 1B, L, M, O, Q, R), tubular in 108 species (59%; Fig. 1C–K, N), and intermediate in 42 species (23%; Fig. 1A, P). The shape of the tubular flowers is mostly straight (parallel sides, e.g., in *Salvia iodantha* Fernald or *S. nervata* M. Martens & Galeotti in Fig. 1C, I), elliptic in outline (Fig. 1G), or funnelform (e.g., in *S. macrophylla* Benth., *S. pauciserrata* Benth., or *S. oppositiflora* Ruiz & Pav. in Fig. 1E, F, N).

Stability of the corolla. The stability of the corolla ranges from being stiff as in, e.g., *Salvia confertiflora*, *S. karwinskii* Benth., or *S. madrensis* Seem. (Fig. 1D,

G, K) to weak as in, e.g., *S. sagittata* Ruiz & Pav. or *S. macrophylla* (Fig. 1E).

Stability of the lower corolla lip. The stability of the lower corolla lip varies from stable, e.g., in *Salvia confertiflora* (Fig. 1D) to weak, e.g., in *S. patens* Cav. or *S. sagittata*.

Lower corolla lip length/position. The length of the lower corolla lip ranges from 41 mm in *Salvia patens* to 1 mm in *S. nervata* (Fig. 1I) and shows diverse positions, being mostly antrorse (e.g., *S. dombeyi*, *S. gravida* Epling, and *S. atrocyanea* Epling in Fig. 1A, L, M), but also deflexed (e.g., *S. oaxacana* Fernald in Fig. 1O) to reflexed (e.g., *S. lasiantha* Benth., *S. macrophylla*, *S. pauciserrata*, and *S. karwinskii* in Fig. 1B, E–G). The lower lips may be additionally cupped with incurved front margins (e.g., *S. confertiflora* and *S. leucantha* Cav. in Fig. 1D, H). The lateral lobes may be oriented vertically (e.g., *S. confertiflora*, *S. leucantha*, and *S. madrensis* in Fig. 1D, H, K). In flowers with weak, very short, reflexed, or deflexed lower lips, the landing of insects is impossible or difficult. The same applies for antrorse lower lips that lengthen the functional tubes (e.g., in *S. confertiflora* and *S. leucantha* in Fig. 1D, H). Antrorse lip positions bent downward either slightly to almost a right angle may offer a potential landing platform; however, bees are excluded by tube length. In species with short flowers, the tubular shape and increased tube length caused by the antrorse lower lips are more abundant than in long-tubed flowers.

Corolla color. The flowers in ornithophilous *Salvia* species are always conspicuous. The color of the corolla is most often red (49%), but also orange, yellow, purple, pink, lavender, violet, and blue, and rarely brownish ochre or red-brown (Fig. 4). A weak color change occurs in *S. graciliramulosa* Epling & Játiva and *S. spathacea* Greene. The calyx is mostly green or sometimes weakly colored in portions. Especially in species with white flowers, the calyx can be more strikingly colored, e.g., mostly purple in *S. leucantha* (Fig. 1H), purple or white/whitish in *S. tomentella* Pohl, or light violet to whitish in *S. divinorum* Epling & Játiva. Several other species have colored calyces and bracts, e.g., red in *S. confertiflora* (Fig. 1D) and *S. regla* Cav., yellow in *S. madrensis* (Fig. 1K), pink in *S. involucrata* Cav., sometimes purple in *S. gravida* and *S. lasiantha* (Fig. 1B), dark red to purple or almost black in *S. spathacea*, violet-black in *S. atrocyanea*, or blue-black or whitish to light green in *S. paramicola* Fern. Alonso. Regarding the geographic distribution, there are no noteworthy characteristics in flower color, except a high percentage of red-flowered taxa in Brazil, whereas blue and dark violet flowers occur mainly in *Salvia* species from the Andes, Mexico, and Central America.

Nectar guides. Nectar guides are usually lacking, but in at least nine species they occur on the lower lip near the entrance and in at least 15 species they are sometimes present. Nectar guides are mostly white and sometimes dark red-blackish; both colors occur in *Salvia exserta* Griseb. The whitish stamens may contrast to a colored corolla, as for example in *S. atrocyanea* (Fig. 1M). In *S. alborosea* Epling & Játiva, the whole lower lip is white.

Nectary length. The nectary length varies from 1 to 5 mm and some nectaries are very voluminous (Table 1A, B).

Nectar. In all species examined, a large to medium volume of nectar with a mostly low to medium sugar concentration was produced (Table 1A, B).

Nectar retention structures. Nectar retention structures at the base of the corolla are rather common in ornithophilous *Salvia* species. In almost all species they appear as slight lateral and horizontal narrowings of the corolla tube (not included in Table 1A, B). In addition, there can be strong lateral or abaxial constrictions (including emarginations or folds), lateral ridges, papillae or hairs, as well as posterior staminal lever arms.

Toothlike structures of staminal connectives. In *Salvia* species of subgenus *Calosphace*, the staminal connectives often form toothlike structures near the abaxial side of their joints. They are relatively large in *S. lasiantha*, *S. atrocyanea*, *S. exserta*, or *S. guaranitica* A. St.-Hil. ex Benth., but small in *S. dombeyi*, minute in *S. gravida*, or even absent as in *S. oppositiflora*. In all ornithophilous *Salvia* flowers, they do not occlude the flower entrance, because they are either arranged laterally (*S. atrocyanea* in Fig. 1M; *S. exserta*) or greatly distal (*S. lasiantha* in Fig. 1B).

Thecae position. The thecae position varies from being enclosed by the upper lip in 101 species (e.g., in *Salvia dombeyi* or *S. atrocyanea* in Fig. 1A, M) to being exserted as much as 43 mm (*S. speciosa* C. Presl ex Benth.) in 64 species (e.g., *S. lasiantha*, *S. iodantha*, *S. macrophylla*, or *S. pauciserrata* in Fig.

Table 1A. Characteristics of the New World ornithophilous *Salvia* species (n = 184).

Salvia spp.	Corolla length, mm	Corolla tube length, mm	Upper lip length, mm	Lower lip length, mm	Lower lip position*	Flower shape*	Nectar retention*	Exposition of thecae, mm	Corolla color*	Corolla color (CMYK)*
acuminata Ruiz & Pav.	59–65	47–50	12–15			b/t		0	Re	
adenophora Fernald	22–29	16–23	5–8	5–8	a, cu, v, lc	t	–	0	Re	M90 Y80 S00
alborosea Epling & Játiva	24–25	17–18	7–8	4	ah, cu?	t (f)		8–16	Re, Pu?	
altimitrata Epling	23	11	12			b	Rl	[4–8]		
altissima Pohl	29–33	16–18	13–15		[a]	b/t	Cb	0	Re	
apparicii Brade & Barb. Per.	40–50	35–40	7	4		t (f) or t			Re	
arbuscula Fernald	21–23	15–17	6	[3–5]	a	t	P	[4–8]	Pu	
arduinervis Urb. & Ekman	21–28	16–21	5–7	3–5	[a and/or d?]	t		5–8	Pi, Lav	
articulata Epling	41–61	28–45	13–16	12	d, a	b/t		0	Pu	
atrocaulis Fernald	44–47	25–30	19–21	17–20	d, a	b		0	Bl-daVi	
atrocyanea Epling	25–48	15–31	10–18	8–17	a, d	b	–	0	Bl-daVi	C99 M80–90 S00–10
ayavacensis Kunth	37–39	27–28	7–10	8–15	a and/or d	t		6–7	Bl-daVi	
bahorucona Urb. & Ekman	19–26	16–21	3–5	2–3	[r, d]	t			Ye, Or, Re	
balaustina Pohl	46–55	33–40	13–22	[27]?	a	b/t		0	Re	
benthamiana Gardner	36–48	20–30	16–18	[12–14]	a	b/t		0	Re	
betulifolia Epling	35–56	23–37	12–19	10–19	a	b/t		0	Re	
blepharophylla Brandegee ex Epling	28–36	18–25	8–11	10–19	mostly d, also r, a	b	Cb	0	Re	M99 Y99 S10
booleana B. L. Turner	30–42	18–27	12–15	10–12	[d]	b		0?	Re	
buchananii Hedge	39–50	24–30	15–20	15–20	a, d	b	Cb	0	Pu	C40 M99 Y10
cacaliifolia Benth.	22–28	17–20	4–10	8–10	ah, v, often cu	t (f)	PL	6–10	Bl(rb)	C95 M75 Y00
camarifolia Benth.	15–24	12–19	3–6	3–6	a, cu, v, lc	b/t		0	Re	
chapadensis E. P. Santos & Harley	42–46	30–33	12–15	8–10		b/t		0	Re	
cinnabarina M. Martens & Galeotti	20–33	15–25	5–8	4–6	a	t	PL	4–9	Re	M99 Y70 S10
clarkcowanii B. L. Turner	26–37	21–28	6–10	4–9	a	t	Cb	3–9	daVi	
coccinea Buc'hoz ex Etl.	20–30	13–22	4–8	10–13	d	t	–	3–9	Re	M99 Y99 S00–20
cocuyana Fern. Alonso	12–15	11–14	1	2–3	a, v	t	PL?	0	Re	
confertiflora Pohl	7–13	5–9	2	2–3	ah, cu, v, lc	t	–	0	Re	M90 Y99 S10
cubensis Britton & P. Wilson	18–25	13–19	5–6		[a]	t			Re	
curtiflora Epling	19–31	17–27	2–4	2–4	ah, v	t	PL	1–3	Re, Pu	C30 M99 S20
curviflora Benth.	28–35	18–22	10–13	8	a	b/t	P	0	Pu	

Table 1A. Continued.

Salvia spp.	Corolla length, mm	Corolla tube length, mm	Upper lip length, mm	Lower lip length, mm	Lower lip position*	Flower shape*	Nectar retention*	Exposition of thecae, mm	Corolla color*	Corolla color (CMYK)*
cyanocephala Epling	28–45	20–36	4–12	5–15	r, possibly d, [a]	t	PL	1–6	Bl-daVi	
cylindriflora Epling	49	43	6	[6]		t		[4]		
darcyi J. Compton	36–44	24–27	12–17	15–20	d, also weakly r	b	P, Cb	0	Re	M90 Y90 S00
diamantina E. P. Santos & Harley	45	28–30	14–15	7–8		b/t		0	Re	
disjuncta Fernald	(18)26–46	(14)20–39	(4)6–13	(4)6–13	a, d, sometimes lc	t	Rl	0	Re	M90–99 Y90–99 S00–10
divinorum Epling & Játiva	28–35	19–27	6–10	5–7	a, cu, v, lc	t		0	Wh (calyx paVi to whitish)	C00 M00 S00 (calyx whitish with C40–45 M45–50 S00)
dombeyi Epling	(85)98–130	(60)80–90	22–30	19–24	a	b/t		0	Re	M99 Y99 S10
dorisiana Standl.	53–64	35–40	19–24	15–23	d, also r	b/t	P, Cb	0	Pi	C20–30 M90 S00–10
dugesiana Epling	31–38	23–28	8–9	[8–9]	[a]	b/t		0	Re	
elegans Vahl	28–39	18–29	8–13	7–12	a, sometimes d	t	–	0–4	Re	M99 Y80 S20
ernesti-vargasii C. Nelson	24–30	20–24	4–6	3–4	d, bc	t	P?	0	Re	
erythrostephana Epling	22–23	17–20	[4–5]	[5–6]	a	t		0	Pi	
espirito-santensis Brade & Barb. Per.	55–60	40–45	18–20	15–16	a	b/t		0	Re	
exserta Griseb.	14–36	10–28	4–9	7–15	r, d	t	H	6–22	Re	M99 Y99 S10
falcata J. R. I. Wood & Harley	26–35	16–33	10–12	5–7	[a]	b/t		0	Re	
florida Benth.	30–42	24–35	5–7	5–8	d	t	PL	8–12	Pi, Pu	M99 Y20 C70
formosa L'Hér.	38–47	23–28	15–18	13–15	d, a	b	P	0	Re	
foveolata Urb. & Ekman	18–28	14–22	4–6	3–5	[d]	t		7–11	Ye	
fruticetorum Benth.	38	32	6			t		[1]?	Re or Pu?	
fulgens Cav.	38–61	25–39	13–24	16–23	a, also d, sometimes r	b	P, weak Cb	0	Re	M99 Y70 S10
funckii Briq.	25–31	18–21	9–11	13–16		t (f)	PL	[13–18]	Bl	
gachantivana Fern. Alonso	12–20	11–19	1	1–3	a and/or d, v	t	PL?	0	Re	
gesneriiflora Lindl. & Paxton	50–66	28–44	15–23	15–24	a, d	b	–	0	Re	M99 Y80 S10, M95–99 Y99 S00

Table 1A. Continued.

Salvia spp.	Corolla length, mm	Corolla tube length, mm	Upper lip length, mm	Lower lip length, mm	Lower lip position*	Flower shape*	Nectar retention*	Exposition of thecae, mm	Corolla color*	Corolla color (CMYK)*
graciliramulosa Epling & Játiva	25–46	18–28	11–18	14–23	a, d	b	P, Cb	0	Re	young/adult: M90–99 Y50–90 S30, M99 Y60 S40, M99 Y50 S20 to old: M90–70 Y00 S30
grandis Epling	22–23	16–17	6	6	[a]	t	P	0	Pi, Pu	
gravida Epling	44–58	27–36	17–22	20–22	a, also d	b	–	0	Re, Pu	C50 M99 S00, C10 M99 S60, C60 M 99 Y60
greggii A. Gray	26–32	18–22	8–11	[13–14]	d, also a, r	b	–	0	Re, Pu	C00 M00 S00 (white cultivar)
grewiifolia S. Moore	18–34	14–20	9–14	9–12	a, v, lc, sometimes cu	t	Cb	0	Re	M99 Y99 S00
guaranitica A. St.-Hil. ex Benth.	30–56	20–37	11–19	10–17	a	b	–	0	Bl-daVi	C99 M85–90 S00
haenkei Benth.	18–50	15–40	5–10	5–8	r	t	–	5–10	Re	M90–99 Y80–99 S10, M90 Y70 S00, M60 Y90 S00
hapalophylla Epling	32–35	26–28	6–7	[4–5]	[d]	t		[5–9]	Re	
harleyana E. P. Santos	8–9	6–8	2	2	[a, v]	t		0	Re	
hatschbachii E. P. Santos	60–64	43–45	17–19	14–17	[a?]	t		0	Re	
heerii Regel	31–32	25–26	6	ca. 6	r	t (f)	PL	[13–20]	Re	
henryi A. Gray	28–39	22–31	6–8	8–9	d, also a	t	–	0–6	Re, rarely Pi, Pu	M 90 Y20 S00 (cult.)
herrerae Epling	16–22	11–17	3–6	2–5	[a, v]	b/t		0	Re	
hidalgensis Miranda	23–58	18–41	5–18	4–14	[r and/or a]	b/t	H?	0	Ye	
hilarii Benth.	40–47	30–34	10–13	[11]		b/t		0	Re	
hirta Kunth	29–32	25	4–6	[4–6]	a	t	PL	[7–13]	Re	
hirtella Vahl	24–33	20–29	4–6	6–10	d, also r	t	P	7–17	Re	M90 Y90 S10
holwayi S. F. Blake	24–31	15–24	5–8	5–6	r/bc, also d, [a]	t	P, Cb	0	Re, Pi	M99 Y80 S00
integrifolia Ruiz & Pav.	35–46	30–40	5–6	[4–6]		t	PL	[4–10]	Or, Re	

Table 1A. Continued.

Salvia spp.	Corolla length, mm	Corolla tube length, mm	Upper lip length, mm	Lower lip length, mm	Lower lip position*	Flower shape*	Nectar retention*	Exposition of thecae, mm	Corolla color*	Corolla color (CMYK)*
involucrata Cav.	33–43	21–35	7–9	7–10	r + d/bc, sometimes a	t	P, Cb	0	Pi	C20 M99 S00
iodantha Fernald	20–27	15–20	5–7	4–5	a, d, r	t	P	5–7	Pu	C40 M90 S00
iodophylla Epling	34–35	27–28	7	[7–8]	[a, r]	t	P	4–6	Re	
itaguassuensis Brade & Barb. Per.	29	23	4	3		t			Re	
iuliana Epling	48	30	18	ca. 13		b		0		
jorgehintoniana Ramamoorthy ex B. L. Turner	40–55	32–45	7–10	5–6	r, d, a	t	PL	5–10	Re	
karwinskii Benth.	26–36	18–27	6–10	3–7	r/bc	t	P, weak Cb	0	Re, Pi	M90–99 Y40–50 S10
lachnaioclada Briq.	17–27	13–22	4–5	3–4	[d]	t		[4–7]	Ye, Or, Re	
lachnostoma Epling	38–43	28–32	10–11	[9]		t		0	Re, Pu	
lanicaulis Epling & Játiva	23–25	18–20	5	[5–8]		t (f)		[7–11]	Re	
lasiantha Benth.	(11)15–26	(6)8–12	(5)6–16	3–12	r, d, sometimes a	b	Rl	3–8	BrOc, Ye, Or, Re, ReBr, Pi, Pu, Vi	M60–80 Y70–99 S10, M80 Y99 S50, M90 Y70 S60, M99 Y70 S40, M99 Y50 S70, M60 Y30 S60, M90 Y40 S50, M80 Y30 S60
lavendula Alain	13–17	10–14	3	3–4		t		[5]	Lav	
leucantha Cav.	16–20	13–17	3–6	3–5	ah, cu, v, lc	t	–	0	Wh (calyx Pu, rarely Wh)	C00 M00 S00 (calyx C70–90 M90–99 Y00–20)
leucocephala Kunth	32–44	20–28	12–19	[9–12]	r	b/t	–	0	Pu	C70 M99 Y50
libanensis Rusby	53–63	33–43	20–23	17–22	a	b/t		0	Re	
lineata Benth.	26–45	20–28	6–12	8–13	a	b	P, Cb	0	Re	M90 Y90 S00
littae Vis.	24–36	15–23	9–14	6–11	r	b	P	0	Pi, Pu	C30–50 M99 Y00–20
lobbii Epling	27–36	21–28	5–8	5–8	d	t (f)	PL	[7–12]	Bl-daVi	

Table 1A. Continued.

Salvia spp.	Corolla length, mm	Corolla tube length, mm	Upper lip length, mm	Lower lip length, mm	Lower lip position*	Flower shape*	Nectar retention*	Exposition of thecae, mm	Corolla color*	Corolla color (CMYK)*
longibracteolata E. P. Santos	14	11	3	3	ah, cu, v, lc			0	Re	
longistyla Benth.	33–45	27–37	6–8	4–9	d, a	t	PL	6–9	Re	M99 Y50–70 S40
macrocalyx Gardner	45–49	30–33	15–16	8–10		b/t		0	Re	
macrophylla Benth.	20–26	11–18	6–13	7–11	r	t (f)	PL	10–15	Bl(rb)	C99 M70 S00
madrensis Seem.	23–35	18–26	4–9	3–9	a, v, lc	t	–	0	Ye	Y80 M10 S10
marci Epling	22–38	14–23	10–18	6–16	[d]	b		0	Pu	
mattogrossensis Pilg.	25–35	20–22	5–6	[3–4]	ah, cu, v, lc	t		0	Re	
medusa Epling & Játiva	28–56	21–46	7–12	6–13		t (f)	PL	8–10	Bl-daVi, sometimes Pu	
melaleuca Epling	35–45	32–38	6–15	12–20	[d, r?]	b/t	PL	4–7	Re	
melissiflora Benth.	14–18	11–16	3–4	[2–3]	[a, also ah]	t		[0–1]?	Re	
mentiens Pohl	28–41	22–34	5–8	5–7	[a]	t		0	Pi, Pu	
microphylla Kunth	20–32	14–20	6–12	7–15	d, also a	b	PL	0	Re, Pu, Pi	C50 M99 Y00, C20–30 M90–99 Y00–40, C10 M99 Y50
miniata Fernald	28–42	20–27	8–15	12–14	d, also cu	b	–	0	Re	M99 Y90 S10, M99 Y90 C20
neovidensis Benth.	29–31	25–26	4–5			t		5–7		
nervata M. Martens & Galeotti	30–44	21–29	8–15	1–3	ah, v	t	PL	0–1	Re, Pu	M99 Y30 S60
nigrescens Alain (nom. illeg.)	25–30	[16–19]	[9–10]			t		[1–3]?	Re	
oaxacana Fernald	32–42	15–21	7–22	12–15	d, r, rarely a	b	Cb	0	Re	M99 Y60–70 S10–20
ombrophila Dusén	22–28	16–21	5–7	5–9	r, d, [a]	b/t		0	Re, Pi?	
oppositiflora Ruiz & Pav.	21–42	16–34	5–11	5–12	a, also ah, v, lc, sometimes cu	t (f)	PL	2–6	Re, Pi	M90 Y90–99 S00
orbignaei Benth.	32–51	18–29	10–23	9–21	d	b	P, Cb	0	Pi, Pu, rarely Wh	C00–30 M80–99 S00, also C00 M60–80 S00, C00 M5–10 S00
orthostachys Epling	12–15	11–14	1	2	d, [a, v]	t	PL?	0	Re	
oxyphora Briq.	30–48	22–38	5–11	7–12	d, a, also bc	t	P, Cl	0	Re, Pi	M90 Y60 S00, M90–99 Y00–30 S00–10

Table 1A. Continued.

Salvia spp.	Corolla length, mm	Corolla tube length, mm	Upper lip length, mm	Lower lip length, mm	Lower lip position*	Flower shape*	Nectar retention*	Exposition of thecae, mm	Corolla color*	Corolla color (CMYK)*
palealis Epling	25–26	17–19	5–6	5–6	[a]	t	P	3–6	Re	
paramicola Fern. Alonso	24–26	18–19	5	[5–6]	[a, cu, lc, d]	t		0	daVi(Black)	
paryskii Skean & Judd	25–31	20–25	5–6	4–5	d	t			Ye, Or	
patens Cav.	40–63	15–28	23–35	27–41	d	b	Cb	0	Bl(rb)	C99 M75 S10
pauciserrata Benth.	25–59	15–46	7–18	9–15	r, d [a]	t (f)	PL, P	7–12	Re	M99 Y99 S10
pavonii Benth.	16–22	12–18	5–6	4–6	[a]	t		0	Ye	
peninsularis Brandegee	21–29	15–23	6–8	6–9	d	b/t		0	Pi, Pu, Lav	
pentstemonoides Kunth & C. D. Bouché	27–40	15–27	11–16	9–11	d, a, also cu, v	b	H	0	Re, Pu, Pi	C40 M99 S60
persicifolia A. St.-Hil.	45–50	30–35	15	8–9		b/t		0	Re	
phaenostemma Donn. Sm.	23–25	17–18	6–7	ca. 6		t		7–8	Bl or daVi	
pichinchensis Benth.	31–43	20–26	11–18	[12–18]	[d]	t	PL	[9–15 and more]	Bl, daVi	
plumosa Ruiz & Pav.	47	35	12	15		b/t	P	0		
pringlei B. L. Rob. & Greenm.	32–44	22–24	15–20	8–10	a, also d	b		0	Pu	
psilantha Epling	34–43	26–33	8–11	[8–9]		t		5–11		
pubescens Benth.	39–68	25–45	14–23	15–23	a	b/t		0	Re	M90 Y99 S10
pulchella DC.	24–30	16–21	7–9	7–11	a, [d?]	b	P, Cb	0	Re	
quitensis Benth.	33–39	27–32	6–8	[5–10]		t	PL	[8–12]	Re	
raveniana Ramamoorthy	32–34	19–22	12	[7–10]	[r]	b	P	0–3	Re, Pu, Pi	
regla Cav.	27–59	19–41	8–22	8–24	a, d	b/t	–	0	Re	M90 Y80 S00
regnelliana Briq.	40–44	27–30	13–14	[10–14]	a	t		[3]?	Re, Pu	
rhodostephana Epling	22–34	15–25	7–9	14–18	d	t (f)	PL	[7–16]	Pi, Pu, paVi, Bl	
rivularis Gardner ex H. B. Fielding	42–53	30–40	12–13	6–15	a	b/t		0	Re	
roemeriana Scheele	24–47	18–39	6–9	6–15	d, sometimes a, r	t	H	0–7	Re	M90–99 Y60–80 S20
rosei Fernald	25–31	18–20	9–11	[8]		b		2–3	Pi, Pu	
rubescens Kunth	20–39	18–31	2–6	8–10	a, also d	t	PL	0–4	Re	M99 Y90 S10
rubrifaux Epling	32–38	24–30	8–11	[8–11]	[a]	b/t		10–13	Re	
rubriflora Epling	25–30	20–22	8–9	8–17	d	t (f)	PL	15–18	Re	
rufula Kunth	16–40	11–25	5–13	4–9	a, [d, r]	b		0	Re	
rusbyi Britton ex Rusby	40–58	29–46	8–14	8–15	d, a	b/t	–	0–11	Re	M90–99 Y99 S00–10

Table 1A. Continued.

Salvia spp.	Corolla length, mm	Corolla tube length, mm	Upper lip length, mm	Lower lip length, mm	Lower lip position*	Flower shape*	Nectar retention*	Exposition of thecae, mm	Corolla color*	Corolla color (CMYK)*
sagittata Ruiz & Pav.	23–31	16–21	5–10	12–18	d	t (f)	PL	8–13	Bl(rb)	C99 M80 Y00
salicifolia Pohl	47–56	32–36	15–20	10–12	[a]	b/t		0	Re	
scabrata Britton & P. Wilson	32–35	20–22	10–14	8–10	a	t		0	Re	
scabrida Pohl	35–48	25–30	10–18	5–8	[a]	b/t		0	Re	
scandens Epling	50–63	38–45	12–18	16	a	b/t	P	0	daVi	
sciaphila (J. R. I. Wood & Harley) Fern. Alonso	35–43				a	b/t	P	0	Pu	
secunda Benth.	9–13	7–10	2–3	2–3	ah, lc, v, cu	t		0	Re	
sellowiana Benth.	42–62	30–45	12–17	11–15	d, a	b/t		0	Re	
sessei Benth.	30–62	20–42	10–22	9–22	a	b/t	–	0	Re	M99 Y90 S10
sigchosica Fern. Alonso	18–24	11–14	7–10	[ca. 10]	[d, r?]	t	[PL?]	9–10	daVi	
spathacea Greene	28–46	22–37	5–10	6–14	d, r	t	sometimes Cb	7–17	Re, Pu, Pi, rarely Ye	M80 Y40 S30–40 (young), M99 Y30(−00) S50 or C20 M99 S10 to C50 M99 S00 (adult)
speciosa C. Presl ex Benth.	20–23	15–19	5–8	10–14	a or d	b/t		[22–43]	Pu, daVi	
speirematoides C. Wright	24–27	18–22	5–6	[3–4]		t		4–6	Re	
splendens Sellow ex Roem. & Schult.	38–49	30–40	8–11	3–6	ah, cu, lc	t	–	0–1	Re	M90–99 Y90–99 S00
sprucei Briq.	30	24	6	[9–10]	d	t	PL	[8–10]	Pi	
squalens Kunth	32–44	22–29	10–17	16–19	d, a	t (f)	PL	2–6	Re, Pi	M99 Y99 S10, M80 Y70 S00
stolonifera Benth.	(34)39–50	(22)30–35	11–16	9–17	a	b	P, Cb	0	Or, Re	
striata Benth.	27–45	19–32	6–13	5–11	ah, cu, v, lc	t (f)	PL	0–5	Re, Pi	M30 Y00–20 S00, M50 Y10 S00, M90 Y90 S00
subhastata Epling	39–43	27–35	11–13	[11–12]	a	b/t		0	Wh, Pi, Ye	
subrotunda A. St.-Hil. ex Benth.	17–29	12–22	4–7	6	d, a	t		3–4	Re	
subrubens Epling	33–34	24	9–10	[10]		t		2–3		
summa A. Nelson	26–48	19–39	7–11	13–17	d, rarely a	t	H	0–2	Pi, Pu	C20 M70 S00
tenuiflora Epling	32–48	22–38	10	[6]	a	t		4–6	Re	

Table 1A. Continued.

Salvia spp.	Corolla length, mm	Corolla tube length, mm	Upper lip length, mm	Lower lip length, mm	Lower lip position*	Flower shape*	Nectar retention*	Exposition of thecae, mm	Corolla color*	Corolla color (CMYK)*
thormannii Urb.	28–33	22–27	6	6		t		6–11	Or, Re	
tolimensis Kunth	22–27	15–16	9–11	[5–7]	[r, d, a]	b	P	0	Pu	
tomentella Pohl	22–23	17–18	5	3–6	ah, cu, v, lc	t		0	Wh (calyx Pu, whitish gray?)	
tortuosa Kunth	(18)28–45	(12)15–26	(6)9–18	(4)8–11	d, r	b	–	0	Pu	
townsendii Fernald	27–34	21–26	6–8	[5]	[a]	t	P	5–9	Pu	
trachyphylla Epling	32–33	25	7–8	10	a	t		[10–11]	Re, Pi	
tubifera Cav.	26–31	22–25	5–7	2–6	r	t	PL	0	Re	M99 Y60 S30
tubiflora Sm.	40–44	30–35	10–11	[6–8]	ah, cu, v, lc	t (f)	PL	[0–7]	Re	
tubulosa Epling	40–47	30–35	10–12	[9–12]		b/t		0	Re	
tuerckheimii Urb.	27–34	24–30	5–7	3–7	[r and/or d]	t		6–10	Or, Re	
uncinata Urb.	20–29	16–26	4–6	3–5	[r or d]	t		[7]	Ye, Or, Re	
unguella Epling	10	9	1	2	[a]	t		0	Re, Pi	
univerticillata Ramamoorthy ex Klitg.	25–36	18–26	7–10	8–10	r/bc	t	P	0	Re	M99 Y60 S30
venulosa Epling	24	18	6	7	[ah, d]	t		0	Re	
verapazana B. L. Turner	20–26	15–20	5–7	5–7	[a]	t		0	Re	
vestita Benth.	65–67	50–52	11–15	14	[a]	b/t		[1–6]		
wagneriana Pol.	18–44	13–34	3–10	2–8	r/bc, also d	t	P, Cb	0	Re, Pu, Pi	M70–90 Y20–40 S00–10
weberbaueri Epling	47–48	35	12–13			b/t		0		
xanthotricha Harley ex E. P. Santos	15–16	13–14	2	1–2	ah, v, lc	t		0	Re	
xeropapillosa Fern. Alonso	13–14	11–13	1	2–4	a, also d, v	t	PL?	0	Re	
Mean and SD	34 ± 12.7	24.7 ± 9.1	9.6 ± 5	9.1 ± 5				3.1 ± 4.7		
Minimum and maximum	7–130	5–90	1–35	1–41				0–43		
n	184	183	183	174				176		

* Refers to the following classification (see Methods): **Lower lip position:** r = reflexed, d = deflexed, a = antrorse (ah = ± horizontal, not flexed), cu = cup-shaped, v = lateral lobes vertical, lc = lower and upper lips close to each other, bc = basal part of lower and upper lips close to each other. **Flower shape:** b = bilabiate, t = tubular (f = tube funnelform), b/t = intermediate. **Nectar retention:** P = papillae, Cl = lateral constriction, Cb = abaxial constriction (sometimes additionally adaxial), Rl = lateral ridges, H = hairs, PL = posterior lever arm, – = none of these characteristics. **Color:** Bl = blue, Bl(rb) = royal blue; BrOc = brownish ochre, Lav = lavender, Or = orange, Pi = pink, Pu = purple, Re = red, ReBr = red-brown, Vi = violet, daVi = dark violet, paVi = pale violet, Wh = white, Ye = yellow. CMYK after Küppers (1999; C: cyan, M: magenta, Y: yellow, K [here S]: black). Square brackets = preliminary data. Blank cells signify no data were available.

Table 1B. Characteristics of the New World ornithophilous *Salvia* species (n = 184).

Salvia spp.	Nectar guides on corolla	Nectar concentration, %*	Nectar volume, µl*	Nectary length, mm	Pedicel length, mm	Growth form*	Distribution*	Taxonomic position
acuminata Ruiz & Pav.					[13–17]	sh (sometimes sc)	PE	subg. *Calosphace*, sect. *Longiflorae*
adenophora Fernald	absent	26.2 ± 2.45 (21.2–30.1), n = 26	l	3	4–8	sh	MX	subg. *Calosphace*, sect. *Holwaya*
alborosea Epling & Játiva	whole lower lip white				[7–16]	ph	PE, EC	subg. *Calosphace*, sect. *Lopeziana*
altimitrata Epling						sh	MX	subg. *Calosphace*, sect. *Mitratae*
altissima Pohl					3–4	ph	BR	subg. *Calosphace*, sect. *Hoehneana*
apparicii Brade & Barb. Per.						ss	BR	subg. *Calosphace*, sect. *Curtiflorae*
arbuscula Fernald					[2–3]	ss	MX	subg. *Calosphace*, sect. *Iodanthae*
arduinervis Urb. & Ekman				2	2–5	sh	HT	subg. *Calosphace*, sect. *Ekmania*
articulata Epling					4–8	sh	BR	subg. *Calosphace*, sect. *Nobiles*
atrocaulis Fernald					5–12	ph	MX	subg. *Calosphace*, sect. *Dusenostachys*
atrocyanea Epling	absent	27.7 ± 3.1 (21.5–32.7), n = 18	l	2–3	3–4	ph	BO, AR	subg. *Calosphace*, sect. *Coeruleae*
ayavacensis Kunth					5–13	ph	PE	subg. *Calosphace*, sect. *Cylindriflorae*
bahorucona Urb. & Ekman				2–3	2–5	sh	HT, DO	subg. *Calosphace*, sect. *Ekmania*
balaustina Pohl					6–12	sh	BR	subg. *Calosphace*, sect. *Nobiles*
benthamiana Gardner					4–5	sh	BR	subg. *Calosphace*, sect. *Nobiles*
betulifolia Epling					2–5	sh	MX	subg. *Calosphace*, sect. *Erythrostachys*
blepharophylla Brandegee ex Epling	absent			3–4	5–10	ph	MX	subg. *Calosphace*, sect. *Brandegeia*
booleana B. L. Turner						ph	MX	subg. *Calosphace*, sect. *Fulgentes*
buchananii Hedge	pale pinkish white stripes	28.2 ± 3.4 (23–41.8), n = 27	10.8 ± 4.7 (4–15.5), n = 6; l	2–3	2–4	ph	probably MX	subg. *Calosphace*

Table 1B. Continued.

Salvia spp.	Nectar guides on corolla	Nectar concentration, %*	Nectar volume, µl*	Nectary length, mm	Pedicel length, mm	Growth form*	Distribution*	Taxonomic position
cacaliifolia Benth.	absent	22.8 ± 3.4 (16.3–30.0), n = 45	7.8 ± 2.9 (2–15.5), n = 32; m	2–3	4–6	ph	MX, GT, HN	subg. *Calosphace*, sect. *Standleyana*
camarifolia Benth.					2–5	ss, sh	CO	subg. *Calosphace*, sect. *Tubiflorae*
chapadensis E. P. Santos & Harley					4–5	ss, sh	BR	subg. *Calosphace*, sect. *Nobiles*
cinnabarina M. Martens & Galeotti	absent			2	2–4	ph	MX, GT, SV, HN	subg. *Calosphace*, sect. *Incarnatae*
clarkcowanii B. L. Turner					3–5	sh	MX	subg. *Calosphace*, sect. *Purpureae*
coccinea Buc'hoz ex Etl.	mostly absent, also small white spots	25.7 ± 1.9 (22–27.8), n = 19	m	2	2–5	ah, ph	? (probably MX/Central America or BR)	subg. *Calosphace*, sect. *Subrotundae*
cocuyana Fern. Alonso					4–5	ph	CO	subg. *Calosphace*, sect. *Rubescentes*
confertiflora Pohl	absent	43 ± 12.3 (23–62), n = 61	m; ca. 3.5	2	2–6	ss	BR	subg. *Calosphace*, sect. *Secundae*
cubensis Britton & P. Wilson						sh	CU	subg. *Calosphace*, sect. *Brittonia*
curtiflora Epling	absent			3	3–4	sh	GT	subg. *Calosphace*, sect. *Curtiflorae*
curviflora Benth.						ph	MX	subg. *Calosphace*, sect. *Purpureae*
cyanocephala Epling	absent or white stripes				9–12	ss, sh	CO	subg. *Calosphace*, sect. *Siphonanthae*
cylindriflora Epling					8–16	sh	PE	subg. *Calosphace*, sect. *Cylindriflorae*
darcyi J. Compton	absent			3	4–12	ph	MX	subg. *Calosphace*, sect. *Holwaya*
diamantina E. P. Santos & Harley					5–8	ph, ss, sh	BR	subg. *Calosphace*, sect. *Nobiles*
disjuncta Fernald	absent	26 ± 4.1 (20.2–32), n = 12	l	2–4	3–9	ss (sc), sh	MX, GT	subg. *Calosphace*, sect. *Holwaya*

Table 1B. Continued.

Salvia spp.	Nectar guides on corolla	Nectar concentration, %*	Nectar volume, µl*	Nectary length, mm	Pedicel length, mm	Growth form*	Distribution*	Taxonomic position
divinorum Epling & Játiva	absent			3–5	4–9	ph	MX	subg. *Calosphace*, sect. *Dusenostachys*
dombeyi Epling	absent		l	3–5	10–34	ss (sc), sh, tr	PE, BO	subg. *Calosphace*, sect. *Longiflorae*
dorisiana Standl.	absent or white/ whitish area		l	4	6–14	ph	HN	subg. *Calosphace*, sect. *Holwaya*
dugesiana Epling					8–10	ss	MX	subg. *Calosphace*, sect. *Secundae*
elegans Vahl	absent	17.6 ± 4.3 (7.5–24), n = 18	m	2–4	2–3	ph, ss	MX	subg. *Calosphace*, sect. *Incarnatae*
ernesti-vargasii C. Nelson					6–10	sh	HN	subg. *Calosphace*
erythrostephana Epling					[5]	ss	GT, SV	subg. *Calosphace*, sect. *Tubiflorae*
espirito-santensis Brade & Barb. Per.						sh	BR	subg. *Calosphace*, sect. *Nobiles*
exserta Griseb.	absent or white/ blackish stripes	25.4 ± 5.9 (12–45), n = 117	l	1–2	2–6	ah	BO, AR	subg. *Calosphace*, sect. *Mineatae*
falcata J. R. I. Wood & Harley					1–2	ss	CO	subg. *Calosphace*, sect. *Tubiflorae*
florida Benth.	absent		l	3–4	6–10	sh (sometimes sc)	PE	subg. *Calosphace*, sect. *Floridae*
formosa L'Hér.					[6–7]	ss	PE	subg. *Calosphace*, sect. *Leonuroideae*
foveolata Urb. & Ekman				2–3	1–4	sh	HT, DO	subg. *Calosphace*, sect. *Ekmania*
fruticetorum Benth.						sh	BR	subg. *Calosphace*, sect. *Curtiflorae*
fulgens Cav.	absent	24.4 ± 2.2 (20–27), n = 15	12.7 ± 3.1 (9–16.5), n = 7; l	3	2–7	ph, ss, sh	MX	subg. *Calosphace*, sect. *Fulgentes*
funckii Briq.					4–7	ss (sometimes sc)	CO, VE	subg. *Calosphace*, sect. *Hastatae*
gachantivana Fern. Alonso				2	2–6	ph, ss	CO	subg. *Calosphace*, sect. *Rubescentes*
gesneriiflora Lindl. & Paxton	absent	26.7 ± 1.9 (22.5–31.2), n = 44	21.1 ± 10.7 (5.5–42.5), n = 17; l	2	5–13	sh	MX	subg. *Calosphace*, sect. *Holwaya*

Table 1B. Continued.

Salvia spp.	Nectar guides on corolla	Nectar concentration, %*	Nectar volume, µl*	Nectary length, mm	Pedicel length, mm	Growth form*	Distribution*	Taxonomic position
graciliramulosa Epling & Játiva	absent or lighter area	31.5 ± 4 (24.6–44), n = 25	1	2–3	5–7	ss	BO	subg. *Calosphace*, sect. *Exiles*
grandis Epling						sh	GT	subg. *Calosphace*, sect. *Steyermarkia*
gravida Epling	absent or white/ light area	23.4 ± 4.4 (11.5–30.5), n = 77	27.1 ± 10.2 (16–50), n = 13; 1	2–4	6–15	ph	MX	subg. *Calosphace*, sect. *Skeptostachys*
greggii A. Gray	absent or white			2–3	[5]	ph, ss	MX, US	subg. *Calosphace*, sect. *Flocculosae*
grewiifolia S. Moore	absent	29.4 ± 6.6 (19–53.5), n = 53	1	3–4	4–7	ss	BR, BO	subg. *Calosphace*, sect. *Hoehneana*
guaranitica A. St.-Hil. ex Benth.	absent			3–4	5–8	ph, ss	BR, PY, UY, AR	subg. *Calosphace*, sect. *Coeruleae*
haenkei Benth.	absent or sometimes white stripes	27.2 ± 2.2 (14–32), n = 144	26.5 ± 12.2 (12–50), n = 16; 1	2–3	6–11	ss	PE, BO	subg. *Calosphace*, sect. *Cylindriflorae*
hapalophylla Epling					2–3	ss	PE	subg. *Calosphace*, sect. *Cylindriflorae*
harleyana E. P. Santos						ss	BR	subg. *Calosphace*, sect. *Secundae*
hatschbachii E. P. Santos						ss	BR	subg. *Calosphace*, sect. *Nobiles*
heerii Regel	white/whitish stripes				[6]	ph	PE	subg. *Calosphace*, sect. *Cylindriflorae*
henryi A. Gray	absent			1	3–4	ph	US, MX	sect. *Heterosphace*
herrerae Epling					[4]	sh	PE	subg. *Calosphace*, sect. *Secundae*
hidalgensis Miranda					2–9	ss	MX	subg. *Calosphace*, sect. *Hidalgenses*
hilarii Benth.					6–10	sh	BR	subg. *Calosphace*, sect. *Nobiles*
hirta Kunth					[5–7]	sh	PE, EC	subg. *Calosphace*, sect. *Cylindriflorae*
hirtella Vahl	absent			2	4–12	ph	EC	subg. *Calosphace*, sect. *Phoeniceae*
holwayi S. F. Blake	absent			4	3–7	ph, ss (sometimes sc)	MX, GT, CR	subg. *Calosphace*, sect. *Holwaya*

Table 1B. Continued.

Salvia spp.	Nectar guides on corolla	Nectar concentration, %*	Nectar volume, µl*	Nectary length, mm	Pedicel length, mm	Growth form*	Distribution*	Taxonomic position
integrifolia Ruiz & Pav.					4–6	sh	PE	subg. *Calosphace*, sect. *Cylindriflorae*
involucrata Cav.	whitish/pink areas	27.8 ± 1.2 (26.2–30.2), n = 20	l	2–3	5–9	ph	MX	subg. *Calosphace*, sect. *Holwaya*
iodantha Fernald	absent	23.1 ± 1.3 (21–25.8), n = 20	m	2	2–4	ph, ss	MX	subg. *Calosphace*, sect. *Iodanthae*
iodophylla Epling					[5–6]	? (ah/ph or sh)	MX	subg. *Calosphace*, sect. *Iodophyllae*
itaguassuensis Brade & Barb. Per.						ss	BR	subg. *Calosphace*, sect. *Curtiflorae*
iuliana Epling					to 15	ph	VE	subg. *Calosphace*, sect. *Nobiles*
jorgehintoniana Ramamoorthy ex B. L. Turner					[mostly 10–15]	ph	MX	subg. *Calosphace*, sect. *Curtiflorae*
karwinskii Benth.	absent			3	8–15	ss (sometimes sc), sh	MX, GT, SV, HN, NI	subg. *Calosphace*, sect. *Holwaya*
lachnaioclada Briq.				2	1–4	sh	HT, DO	subg. *Calosphace*, sect. *Ekmania*
lachnostoma Epling						sh	PE	subg. *Calosphace*, sect. *Longiflorae*
lanicaulis Epling & Játiva					5–6	sh	PE	subg. *Calosphace*, sect. *Cylindriflorae*
lasiantha Benth.	absent			2–3	1–4	sh	MX, GT, CR	subg. *Calosphace*, sect. *Mitratae*
lavendula Alain					4	sh	DO	subg. *Calosphace*
leucantha Cav.	absent			2	2–3	ph, ss	MX	subg. *Calosphace*, sect. *Albolanatae*
leucocephala Kunth	absent				[2–4]	sh	EC	subg. *Calosphace*, sect. *Leucocephalae*
libanensis Rusby					5–25	sh	CO	subg. *Calosphace*, sect. *Erythrostachys*
lineata Benth.	absent			2	3–4	ph	MX	subg. *Calosphace*, sect. *Fulgentes*
littae Vis.	absent			2	1–3	ph, ss	MX	subg. *Calosphace*, sect. *Purpureae*

Table 1B. Continued.

Salvia spp.	Nectar guides on corolla	Nectar concentration, %*	Nectar volume, µl*	Nectary length, mm	Pedicel length, mm	Growth form*	Distribution*	Taxonomic position
lobbii Epling					5–7	sh	EC, PE	subg. *Calosphace*, sect. *Siphonanthae*
longibracteolata E. P. Santos						ss	BR	subg. *Calosphace*, sect. *Secundae*
longistyla Benth.	absent	25.9 ± 1.6 (20–28), n = 22	l	3–4	6–17	ph, ss, sh	MX	subg. *Calosphace*, sect. *Curtiflorae*
macrocalyx Gardner					5–8	sh	BR	subg. *Calosphace*, sect. *Nobiles*
macrophylla Benth.	absent	24 ± 1.4 (20.5–26), n = 15	27.7 ± 1.6 (26.5–29.5), n = 3; l	3	4–7	ss	CO, EC, BO, PE	subg. *Calosphace*, sect. *Hastatae*
madrensis Seem.	absent			3–4	9–16	ph	MX	subg. *Calosphace*, sect. *Longipes*
marci Epling					[3–7]	ph, ss, sh	MX	subg. *Calosphace*, sect. *Peninsulares*
mattogrossensis Pilg.						sh	BR	subg. *Calosphace*, sect. *Secundae*
medusa Epling & Játiva					15–32(40)	ss	PE	subg. *Calosphace*, sect. *Siphonanthae*
melaleuca Epling					3–15	ss, sh	CO	subg. *Calosphace*, sect. *Rubescentes*
melissiflora Benth.					2–5	ph	BR	subg. *Calosphace*, sect. *Secundae*
mentiens Pohl						ph	BR	subg. *Calosphace*, sect. *Curtiflorae*
microphylla Kunth	white/light areas or absent			3	2–5	ph, ss, sh	MX, US, GT?	subg. *Calosphace*, sect. *Fulgentes*
miniata Fernald	absent			2	2–4	sh	MX, GT, BZ	subg. *Calosphace*, sect. *Silvicolae*
neovidensis Benth.					3–4	ph	BR	subg. *Calosphace*, sect. *Curtiflorae*
nervata M. Martens & Galeotti	absent			3	3–5	sh	MX, GT	subg. *Calosphace*, sect. *Curtiflorae*
nigrescens Alain (nom. illeg.)					3–8	sh	CU	subg. *Calosphace*
oaxacana Fernald	absent			1	[2–3]	sh	MX	subg. *Calosphace*, sect. *Conzattiana*

Table 1B. Continued.

Salvia spp.	Nectar guides on corolla	Nectar concentration, %*	Nectar volume, µl*	Nectary length, mm	Pedicel length, mm	Growth form*	Distribution*	Taxonomic position
ombrophila Dusén					3–5	sh	BR	subg. *Calosphace*, sect. *Tubiflorae*
oppositiflora Ruiz & Pav.	absent		l	2–3	4–8	ph, ss	PE	subg. *Calosphace*, sect. *Biflorae*
orbignaei Benth.	absent or white/light area	30 ± 2.2 (25.2–37.8), n = 66	20.3 ± 4.6 (13–28.5), n = 13; l	3	4–19	ss	BO	subg. *Calosphace*, sect. *Pavonia*
orthostachys Epling					2–4	ph, ss	CO	subg. *Calosphace*, sect. *Rubescentes*
oxyphora Briq.	absent, rarely (?) white area	31.8 ± 2 (28.2–38.6), n = 30	30.3 ± 9.7 (20–53), n = 19; l	2–4	3–4	ph	BO	subg. *Calosphace*, sect. *Tuberosae*
palealis Epling					[2–4]	ph	MX	subg. *Calosphace*, sect. *Pedicellata*
paramicola Fern. Alonso						ph	CO	subg. *Calosphace*, sect. *Rubescentes*
paryskii Skean & Judd				2–3	3–8	sh	HT	subg. *Calosphace*, sect. *Ekmania*
patens Cav.	white spots, stripes, also pale	24.9 ± 3.5 (10.4–30.3), n = 38	l	2–3	5–9	ph	MX	subg. *Calosphace*, sect. *Blakea*
pauciserrata Benth.	absent	24.8 ± 1.2 (22.8–28), n = 20	13.8 ± 4.9 (9–20), n = 5; l	2–3	3–10	ss, sh	CO, PE, EC, VE, CR	subg. *Calosphace*, sect. *Flexuosae*
pavonii Benth.					3–6	ss	PE	subg. *Calosphace*, sect. *Punctatae*
peninsularis Brandegee					[5–6]	ph, ss, sh	MX	subg. *Calosphace*, sect. *Peninsulares*
pentstemonoides Kunth & C. D. Bouché						ph	US	sect. *Eusphace*/related to sect. *Salviastrum*
persicifolia A. St.-Hil.						sh	BR	subg. *Calosphace*, sect. *Nobiles*
phaenostemma Donn. Sm.					8–10	sh	GT	subg. *Calosphace*, sect. *Sulcatae*
pichinchensis Benth.	white area				8–10	ph, sh	EC	subg. *Calosphace*, sect. *Siphonanthae*
plumosa Ruiz & Pav.					[10–15]	ss	PE	subg. *Calosphace*, sect. *Leonuroideae*
pringlei B. L. Rob. & Greenm.					5	ss	MX	subg. *Calosphace*, sect. *Tubiflorae*

Table 1B. Continued.

Salvia spp.	Nectar guides on corolla	Nectar concentration, %*	Nectar volume, µl*	Nectary length, mm	Pedicel length, mm	Growth form*	Distribution*	Taxonomic position
psilantha Epling					4–6	ph	PE	subg. *Calosphace*, sect. *Cylindriflorae*
pubescens Benth.	absent		1	3	2–4	sh	MX	subg. *Calosphace*, sect. *Erythrostachys*
pulchella DC.	absent				3–6	ph, ss	MX	subg. *Calosphace*, sect. *Fulgentes*
quitensis Benth.					5–10	sh	EC	subg. *Calosphace*, sect. *Cylindriflorae*
raveniana Ramamoorthy					[2–3]	ph	MX	subg. *Calosphace*, sect. *Purpureae*
regla Cav.	absent, rarely small white spot			3	1–8	sh, sometimes tr	MX, US	subg. *Calosphace*, sect. *Erythrostachys*
regnelliana Briq.					4–6	ss	BR	subg. *Calosphace*, sect. *Skeptostachys*
rhodostephana Epling					3	ph	PE	subg. *Calosphace*, sect. *Hastatae*
rivularis Gardner ex H. B. Fielding					6–8	sh	BR	subg. *Calosphace*, sect. *Nobiles*
roemeriana Scheele	absent	24.4 ± 3.5 (18.8–32.5), n = 58	1	2	3–4	ph	US, MX	sect. *Heterosphace*
rosei Fernald					[3–5]	sh	MX	subg. *Calosphace*, sect. *Pruinosae*
rubescens Kunth	absent			4	3–12	ss	CO, VE	subg. *Calosphace*, sect. *Rubescentes*
rubrifaux Epling					[4–5]	ph	PE, EC	subg. *Calosphace*, sect. *Cylindriflorae*
rubriflora Epling					2–5	ss	CO	subg. *Calosphace*, sect. *Hastatae*
rufula Kunth					1–5	ss	CO, EC	subg. *Calosphace*, sect. *Killipiana*
rusbyi Britton ex Rusby	absent			2–3	3–6	ss	PE, BO	subg. *Calosphace*, sect. *Cylindriflorae*
sagittata Ruiz & Pav.	white stripes or absent	24.5 ± 2.4 (17.8–31.2), n = 28	6.9 ± 4.1 (2.5–13.5), n = 5; m	2	2–5	ph	PE, CO, EC	subg. *Calosphace*, sect. *Hastatae*
salicifolia Pohl					8–10	sh	BR	subg. *Calosphace*, sect. *Nobiles*

Table 1B. Continued.

Salvia spp.	Nectar guides on corolla	Nectar concentration, %*	Nectar volume, µl*	Nectary length, mm	Pedicel length, mm	Growth form*	Distribution*	Taxonomic position
scabrata Britton & P. Wilson					5	sh	CU	subg. *Calosphace*, sect. *Muricatae*
scabrida Pohl					3–4	ph	BR	subg. *Calosphace*, sect. *Nobiles*
scandens Epling					[5]	sh (sometimes sc)	PE	subg. *Calosphace*, sect. *Weberbaueria*
sciaphila (J. R. I. Wood & Harley) Fern. Alonso						ph	CO	subg. *Calosphace*, sect. *Carneae*
secunda Benth.					3–4	sh	BR	subg. *Calosphace*, sect. *Secundae*
sellowiana Benth.					4–6	sh	BR	subg. *Calosphace*, sect. *Nobiles*
sessei Benth.	absent		1	2–3	2–7	sh, sometimes tr	MX	subg. *Calosphace*, sect. *Erythrostachys*
sigchosica Fern. Alonso	white stripes				3–4	ph or ss	EC	subg. *Calosphace*, sect. *Siphonanthae*
spathacea Greene	absent	20 ± 5.34 (6.8–25.4), n = 23	32.6 ± 16.3 (13–51), n = 10; 1	2–4	0–2	ph	US	sect. *Audibertia*
speciosa C. Presl ex Benth.					8–15	ss	PE	subg. *Calosphace*, sect. *Macrostachyae*
speirematoides C. Wright					[5]	sh	CU	subg. *Calosphace*, sect. *Brittonia*
splendens Sellow ex Roem. & Schult.	absent		1	4	5–6	ph	BR	subg. *Calosphace*, sect. *Secundae*
sprucei Briq.	white area or absent				8–10	sh	EC	subg. *Calosphace*, sect. *Cylindriflorae*
squalens Kunth	absent or pale whitish area		1	3	6–7	ph	PE, EC	subg. *Calosphace*, sect. *Biflorae*
stolonifera Benth.				2	2–4	ph	MX	subg. *Calosphace*, sect. *Holwaya*
striata Benth.	absent	21.2 ± 1.8 (17.6–23.1), n = 22	1	2–3	3–9	ss	PE	subg. *Calosphace*, sect. *Biflorae*
subhastata Epling					10–12	ph to sh	MX	subg. *Calosphace*, sect. *Sphacelioides*
subrotunda A. St.-Hil. ex Benth.	white spots/stripes (always?)				3–6	ah	BR, PY, AR	subg. *Calosphace*, sect. *Subrotundae*

Table 1B. Continued.

Salvia spp.	Nectar guides on corolla	Nectar concentration, %*	Nectar volume, µl*	Nectary length, mm	Pedicel length, mm	Growth form*	Distribution*	Taxonomic position
subrubens Epling					6–7	? (ph or ss or sh)	GT	subg. *Calosphace*, sect. *Floridae*
summa A. Nelson	absent, or white/ pink-purple dots			1–2	6	ph	US, MX	sect. *Heterosphace*
tenuiflora Epling					4–5	sh	BR	subg. *Calosphace*, sect. *Curtiflorae*
thormannii Urb.				2	2–6	sh	DO	subg. *Calosphace*, sect. *Ekmania*
tolimensis Kunth						ss	CO	subg. *Calosphace*, sect. *Purpureae*
tomentella Pohl					[3]	ph	BR	subg. *Calosphace*, sect. *Albolanatae*
tortuosa Kunth					3–5	sh	CO, EC	subg. *Calosphace*, sect. *Tubiflorae*
townsendii Fernald					2–4	ph	MX	subg. *Calosphace*, sect. *Iodanthae*
trachyphylla Epling					4–6	sh	EC	subg. *Calosphace*, sect. *Cylindriflorae*
tubifera Cav.	absent			2	1–2	ph, ss	MX, GT	subg. *Calosphace*, sect. *Curtiflorae*
tubiflora Sm.					5–7	ph, ss	PE, CL	subg. *Calosphace*, sect. *Biflorae*
tubulosa Epling						sh	PE	subg. *Calosphace*, sect. *Longiflorae*
tuerckheimii Urb.				3	2–9	sh	DO	subg. *Calosphace*, sect. *Ekmania*
uncinata Urb.				2–3	2–10	sh	DO	subg. *Calosphace*, sect. *Ekmania*
unguella Epling					[5]	ss	EC	subg. *Calosphace*, sect. *Secundae*
univerticillata Ramamoorthy ex Klitg.	absent		l	2	4–7	ph	MX	subg. *Calosphace*, sect. *Holwaya*
venulosa Epling					6–7	ss	CO	subg. *Calosphace*, sect. *Tubiflorae*

Table 1B. Continued.

Salvia spp.	Nectar guides on corolla	Nectar concentration, %*	Nectar volume, µl*	Nectary length, mm	Pedicel length, mm	Growth form*	Distribution*	Taxonomic position
verapazana B. L. Turner					4–6	ph (?)	GT	subg. *Calosphace*
vestita Benth.						ss, sh	PE probably	subg. *Calosphace*, sect. *Longiflorae*
wagneriana Pol.	whitish/pink area			3	2–10	ph, ss	MX, GT, SV, NI, CR, PA	subg. *Calosphace*, sect. *Holwaya*
weberbaueri Epling					6–9	sh	PE	subg. *Calosphace*, sect. *Longiflorae*
xanthotricha Harley ex E. P. Santos					4–5	ss	BR	subg. *Calosphace*, sect. *Secundae*
xeropapillosa Fern. Alonso					[2–5]	ph	CO	subg. *Calosphace*, sect. *Rubescentes*
Mean and SD		26.2 ± 4.6	18.6 ± 9.8	2.6 ± 0.7	5.9 ± 3.4			
Minimum and maximum		6.8–62	2–53	1–5	0–34(40)			
n		27	13	72	162			

* Refers to the following classification (see Methods): **Nectar concentration** (average, SD, range). **Nectar volume** (average, SD, range): m = medium (about 3–10 µl), l = large (> 10 µl). **Growth form**: ah = annual herb, ph = perennial herb, ss = subshrub, sh = shrub, tr = small tree, sc = scandent. **Countries**: Argentina = AR, Belize = BZ, Bolivia = BO, Brazil = BR, Chile = CL, Colombia = CO, Costa Rica = CR, Cuba = CU, Dominican Republic = DO, Ecuador = EC, El Salvador = SV, Guatemala = GT, Haiti = HT, Honduras = HN, Mexico = MX, Nicaragua = NI, Panama = PA, Paraguay = PY, Peru = PE, United States of America = US, Uruguay = UY, Venezuela = VE. Square brackets = preliminary data. Blank cells signify no data were available.

1B, C, E, F). In 11 species the position of the thecae is variable (Table 1A, B).

Flower scent. No noticeable flower scent was found.

Pedicels. The pedicels are mostly flexible, and their length ranges from 34 mm in *Salvia dombeyi* to being absent in *S. spathacea.*

Growth form. As to the growth form, almost all bird-pollinated *Salvia* species (97%) are perennial herbs, subshrubs, or shrubs. Only *S. exserta* and *S. subrotunda* A. St.-Hil. ex Benth. are annuals, while *S. coccinea* Buc'hoz ex Etl. varies from annual to perennial. Three species (*S. dombeyi*, *S. regla*, *S. sessei* Benth.) are scandent subshrubs, shrubs, or sometimes small trees.

Distribution. The ornithophilous sages show a wide distribution in the New World, reaching from California to Chile and Argentina (Fig. 5, Table 1A, B). Comparing the different countries, Mexico has the largest number of ornithophilous species (57 to 58 spp.) and ornithophilous endemics (41 to 42 spp.). However, considering the total number of *Salvia* species within the country (about 300 spp., the largest species number within a single country), the relative percentage of the ornithophilous species is relatively low (about 19%) compared to other countries.

Centers of diversity for the bird-pollinated species of *Salvia* are (Fig. 5): (1) the central and southern highlands of Mexico and Guatemala; (2) the northern part of the South American Andes (Colombia, Ecuador, Peru, the latter two with about half of the species being bird pollinated); and (3) the southern part of Brazil with more than 50% bird-pollinated species (especially southeastern Brazil, with 25 of the 35 Brazilian species, all endemic to the country). The ornithophilous species in Cuba and Hispaniola (including Haiti and the Dominican Republic) are also all endemic. Relative to a country area, El Salvador, Guatemala, Haiti, and the Dominican Republic have the highest density of ornithophilous sages by species number.

Habitat. Bird-pollinated *Salvia* species occur in all habitats from rainforests to at least mesic habitats in deserts from ca. 200 to 4000 m in elevation. They mainly occur in the highlands of the American cordilleras at elevations from ca. 1500 to 3000 m, and in southeastern Brazil from ca. 1000 to 1500 m.

Systematics. In terms of systematics, most of the New World ornithophilous sages belong to the widespread group *Salvia* subg. *Calosphace* (179 spp. in 56 sections). Three species (*S. henryi* A. Gray, *S. roemeriana* Scheele, *S. summa* A. Nelson) belong to *Salvia* sect. *Heterosphace* Benth. (Arizona to central Mexico), *S. spathacea* (California) to section *Audibertia* (Benth.) Epling, and *S. pentstemonoides* Kunth & C. D. Bouché (Texas) to section *Eusphace* Benth. (see Table 1A, B).

MELITTOPHILOUS SPECIES

Most of the New World sages allow bees to pollinate the flowers (58%; Appendix 2, Fig. 6A–I). Because their flowers correspond in their proportions with bees, provide a landing platform, have in general short corolla tubes, and deposit pollen on the bee's body, we classify them as melittophilous. Altogether, 65 species of this group were seen as living plants (33 at natural localities, 54 cultivated in botanical gardens and nurseries). Pollinating bees were observed at *Salvia stachydifolia* C. Presl ex Benth., *S. rypara* Briq. subsp. *platystoma* (Epling) J. R. I. Wood, *S. cuspidata* Ruiz & Pav. subsp. *bangii* (Rusby) J. R. I. Wood, *S. sophrona* Briq., *S. carduacea* Benth., *S. apiana* Jeps., *S. mellifera* Greene, *S. leucophylla* Greene, *S. dorrii* (Kellogg) Abrams, *S. munzii* Epling, *S. columbariae* Benth., and other species not listed in detail.

Flowers of this group share the following traits:

Corolla tube length. The corolla tube is short (≤ 2 cm), enabling the bees to reach the nectar at the base of the corolla.

Corolla color. The color of the corolla is often blue and violet, but also white, pink, purple (Fig. 6A–I), or rarely yellowish. Nectar guides are often found at the flower entrance (Fig. 6C, G, H).

Staminal connectives. A peculiar feature of many bee-pollinated *Salvia* species in subgenus *Calosphace* is the presence of distinct ventral teeth or barriers at the connectives. The latter may be large and contribute to occlude the entrance. In *S. rypara* subsp. *platystoma* (Fig. 6D) and *S. pusilla* Fernald, for example, the lever mechanism is triggered by pushing back these barriers. In species like *S. amplifrons* Briq. and *S. cuspidata* subsp. *bangii*, the ventral formations are laterally arranged.

Pollen sacs. The pollen sacs of most species are enclosed by the upper lip (Fig. 6A–D, I). Exceptions (exposed pollen sacs) are found in all species of sections *Echinosphace* Benth. (Fig. 6E, G) and *Audibertia* (Fig. 6F, H), and in very few species of

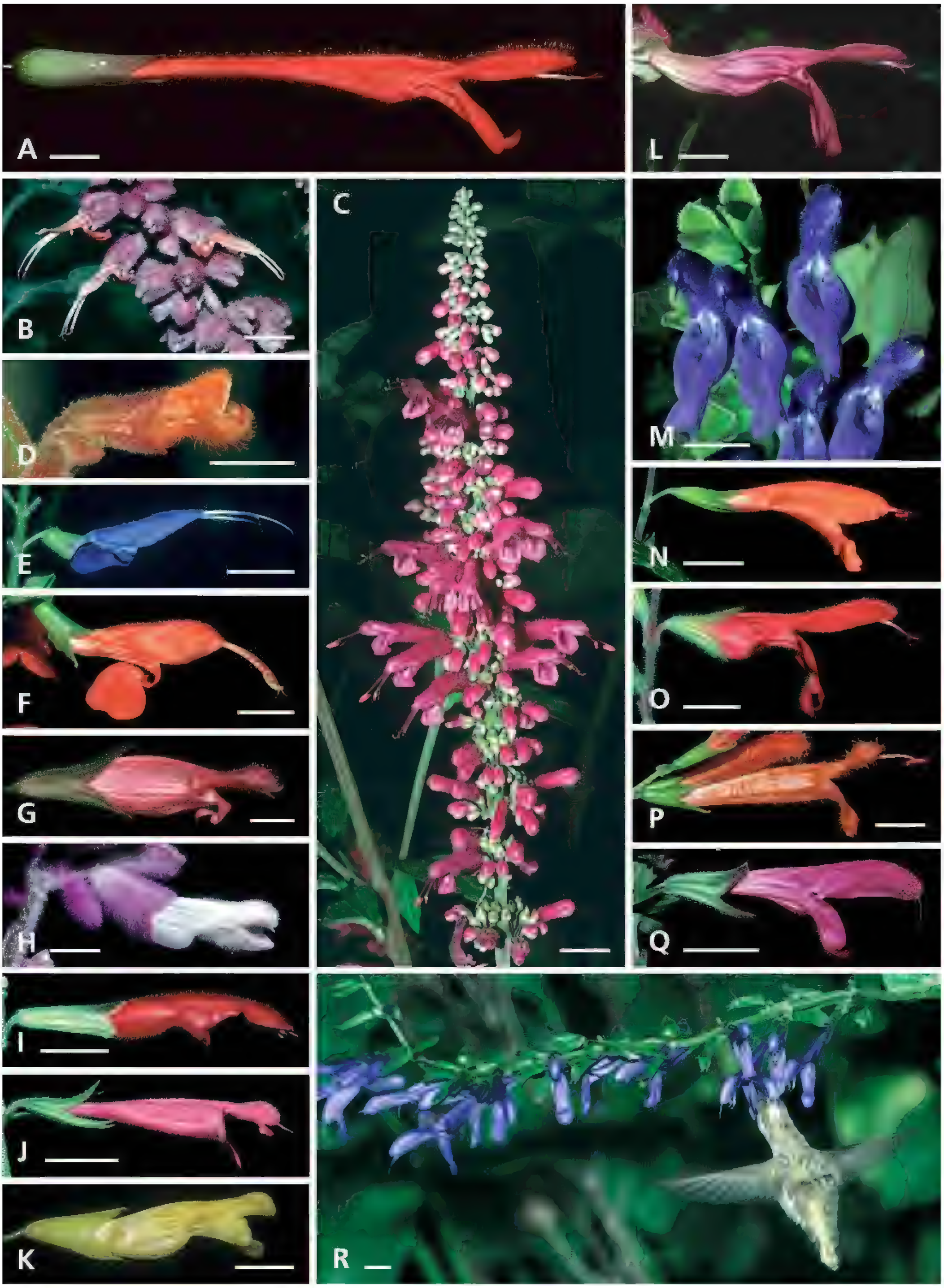

Figure 1. Diversity of ornithophilous *Salvia* flowers. —A. *S. dombeyi* with the largest flower in the genus. —B. *S. lasiantha*, view of inflorescence, with flowers having greatly exserted thecae and reflexed lower lips. —C. *S. iodantha* inflorescence bearing long-tubed flowers with greatly exserted thecae. —D. *S. confertiflora* flower with cup-shaped lower lip. E, F. Flowers with reflexed lower lips and greatly exserted thecae. —E. *S. macrophylla*. —F. *S. pauciserrata*. —G. *S. karwinskii*, elliptic in outline with reflexed lower lip. —H. *S. leucantha* flower with antrorse lower lip lengthening the corolla tube. —I. *S. nervata* flower tubular with very short lower lip. J, K. Relatively long-tubed flowers. —J. *S. henryi*, usually red. —K. *S. madrensis*.

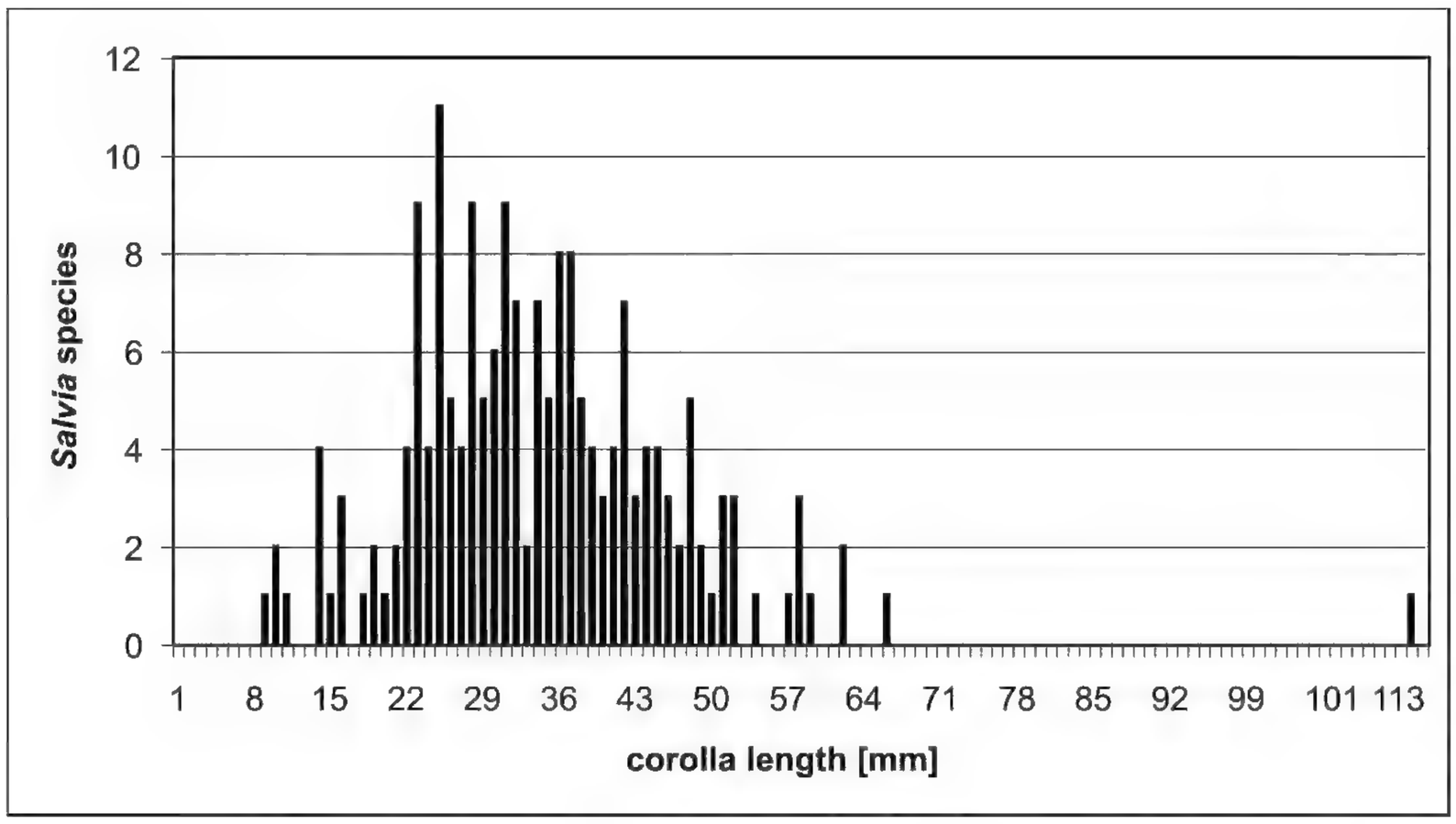

Figure 2. Corolla length in ornithophilous *Salvia* species. Lengths were calculated from the average of the minimum and maximum values listed in Table 1A and B. Sample size, n = 184.

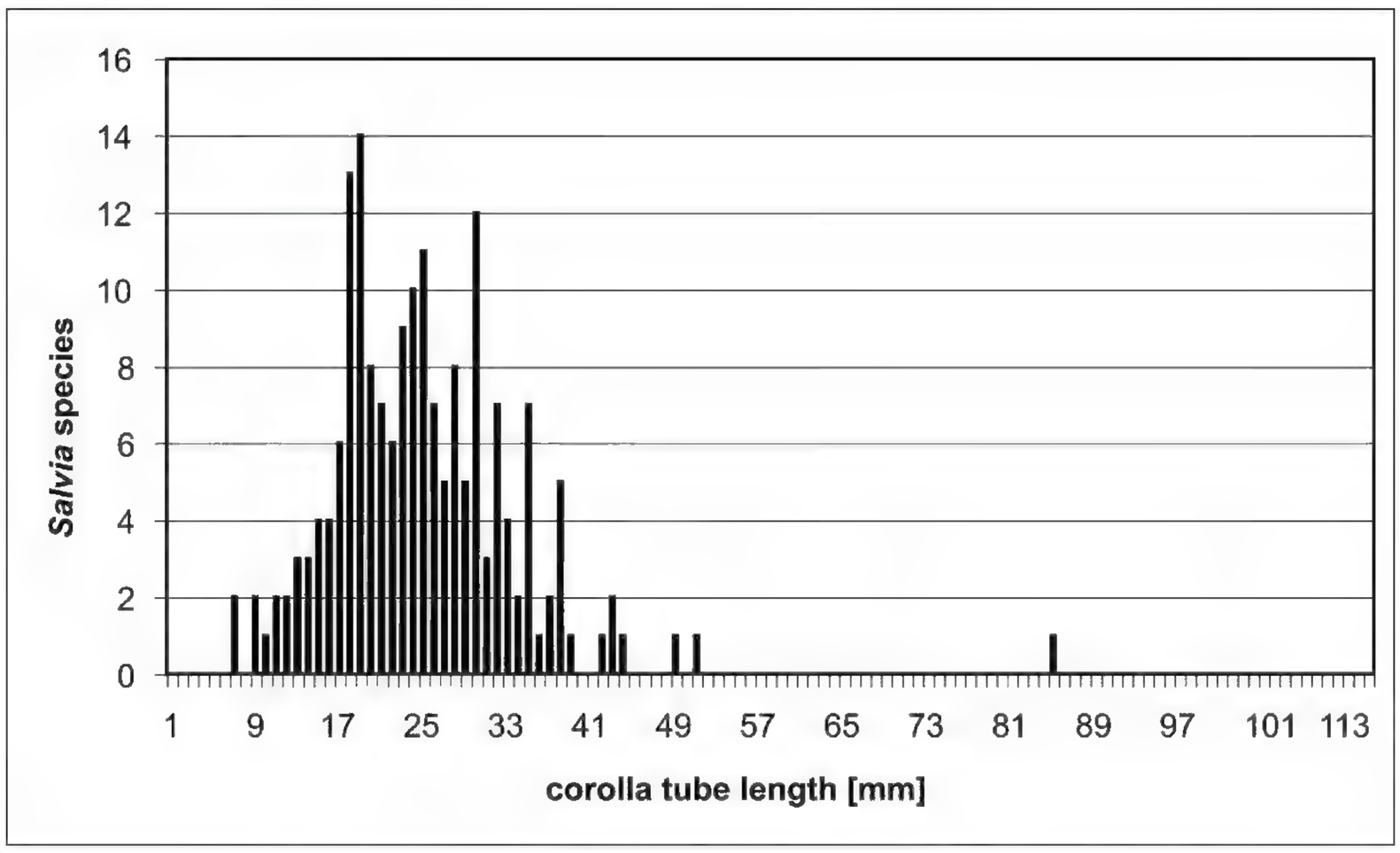

Figure 3. Corolla tube length in ornithophilous *Salvia* species. Lengths were calculated from the average of the minimum and maximum values listed in Table 1A and B. Sample size, n = 183.

Salvia subg. *Calosphace* (e.g., *S. rhombifolia* Ruiz & Pav., *S. tafallae* Benth., *S. palifolia* Kunth, *S. paposana* Phil.).

Staminal lever mechanism. Usually, the staminal lever mechanism is functional (e.g., *Salvia stachydifolia*, *S. texana* (Scheele) Torr., *S. rypara* subsp. *platystoma*). It is lacking only rarely, as for instance in *S. carduacea* or *S. apiana*.

Connivent lips at flower entrance. In *Salvia betonica* Schult. and *S. lavanduloides* Kunth (section *Lavanduloideae* Epling of *Salvia* subg. *Calosphace*), the flower entrance is more or less closed and

←
L, M. Bilabiate flowers with long tubes and large lips. —L. *S. gravida*. —M. *S. atrocyanea*. —N. *S. oppositiflora* flower funnelform with slightly exserted thecae. —O. *S. oaxacana* flower with deflexed lower lip. —P. *S. rusbyi* flower long-tubed with exserted thecae (the species also has individuals with thecae enclosed by the upper lip). —Q. *S. pentstemonoides* flower bilabiate with tube of medium length and relatively long upper lip. —R. *S. guaranitica* visited by the hovering hummingbird *Calypte costae* with thecae and pollen on the bird's head. Scale bars: A–C, E, F, I–R = 1 cm; D, G, H = 0.5 cm.

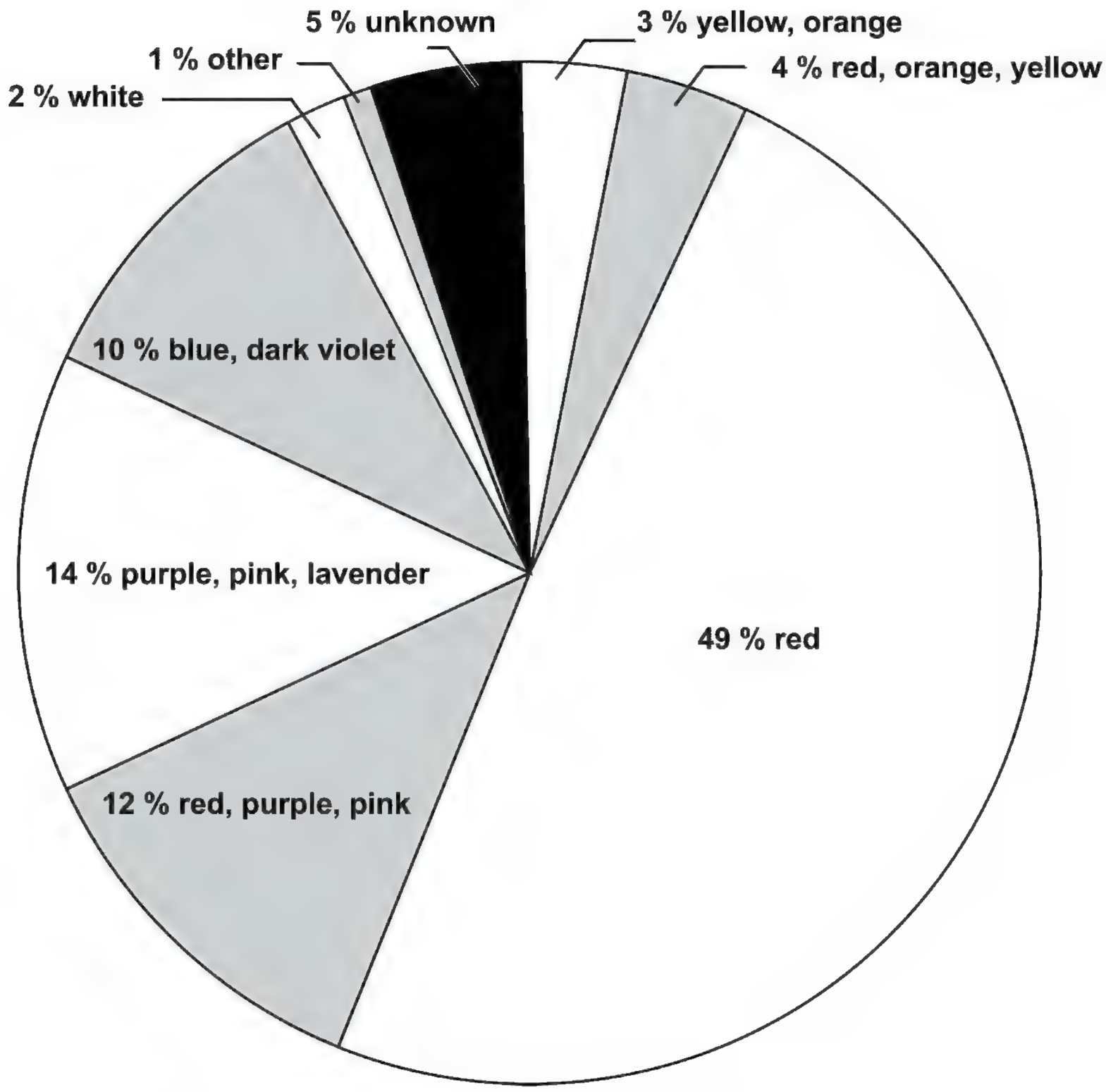

Figure 4. Corolla color of ornithophilous *Salvia* species (see Table 1A, B).

concealed by connivent lips (Fig. 6I), a feature not found in ornithophilous sages.

Arrangement of flowers. The flowers of the species investigated are usually flexibly arranged (e.g., *Salvia amplifrons*, *S. uliginosa* Benth., *S. rypara* subsp. *platystoma*), but stable enough to bear the bees' weight. If they are more stiffly arranged, they may have shorter (and more stable) pedicels or may be densely arranged in the inflorescence (e.g., *S. betonica*, *S. dorrii*, *S. leucophylla*).

Nectaries and nectar. Nectaries are in general smaller than those in ornithophilous flowers, producing only small amounts of highly concentrated nectar (e.g., *Salvia stachydifolia*, *S. rypara* subsp. *platystoma*).

Flower scent. No noticeable flower scent was found in the species examined, except a honeylike or sweetish scent in *Salvia leucophylla*, *S. apiana*, *S. californica* Brandegee, and *S. carduacea*.

Nonpollinating visitors. Hummingbirds were (rarely) observed to visit the flowers (*Salvia* cf. *longispicata* M. Martens & Galeotti). In addition to pollinators, nectar-stealing and/or pollen-stealing bees were observed at, e.g., *S. rypara* subsp. *platystoma*, *S. stachydifolia*, *S. apiana*, and *S. carduacea*, nectar-stealing butterflies at *S. engelmannii* A. Gray, *S. leucophylla*, *S. columbariae*, and *S. carduacea*, and a hawkmoth at *S. carduacea*.

Distribution. Compared to ornithophilous species, the bee-pollinated sages have a wider distribution and are more abundant (e.g., in Mexico and the United States, in Argentina, Paraguay, and Panama; Fig. 5). They show a wider altitudinal range, but mainly occur in slightly lower elevations than the ornithophilous species (for instance, in Colombia and Ecuador and at least some areas in Mexico, such as the Sierra Manantlán and the Valle de México, and Brazil).

PSYCHOPHILOUS SPECIES

Salvia whitehousei Alziar (section *Salviastrum* (Scheele) Gray) definitely excludes bees by its very long (34.8 ± 4.4 mm, range 26–44 mm, n = 33 flowers) and relatively narrow corolla tube (Fig. 6J). The flowers also differ in color, shape, and symmetry from ornithophilous ones. They are basically mono-

Figure 5. Approximate distribution area of the genus *Salvia* in the New World (gray) and its ornithophilous species (diagonal lines). The first number in the slashed pairs refers to the total number of ornithophilous species per country, and the second number refers to the total number of endemics in that group. Below these paired numbers, the approximate percentage of ornithophilous species per country is indicated. Note that the widespread *S. coccinea* (southern United States to southern South America) is not considered because its natural distribution is unclear (perhaps Mexico/Central America or Brazil).

symmetrical, but almost radial in appearance because all petal lobes spread at a right angle, forming a disc at the end of the corolla tube (lobes 7–13 mm long). The flowers are light pink to lavender (color values: C10–30 M10–50 S00) with two white spots below the flower entrance most likely acting as nectar guides. The thecae in the flower entrance are whitish and thus likewise conspicuous. The staminal joint is functional, but the connective arms are too short to block the entrance for an insect's proboscis. A light,

Figure 6. Diversity of *Salvia* flowers, being melittophilous (A–I), psychophilous (J), and not clearly assignable to a syndrome (K–Q). —A. *S. stachydifolia* flowers with pollen sacs enclosed by the upper lip, short corolla tubes, and large lower lips as landing platform. —B, C. *S. texana* flowers with large lower lips possessing white nectar guides. —D. *S. rypara* subsp. *platystoma* flowers short-tubed, showing large connective outgrowths in the flower entrance. E–H. Flowers with exposed thecae and large lower lips. —E. *S. carduacea*. —F. *S. apiana*. —G. *S. californica*. —H. *S. columbariae*, the latter two with white and patterned nectar guides on the lower lips. —I. *S. betonica* flower entrance more or less closed and concealed by connivent lips. —J. *S. whitehousei* inflorescence view bearing long-tubed salverform flowers with white nectar guides. K, L. Flowers with melittophilous and ornithophilous characters. —K. The variably sized *S. concolor* flower. —L. *S. aspera*. —M, N. *S. mohavensis* flowers with ornithophilous and psychophilous characters, having long, narrow corolla tubes, lips spreading at a right angle to the tube (M), and exserted thecae, varying sometimes in the width of the corolla tube, orientation of corolla lips, and corolla color (N). —O. *Salvia retinervia* flowers with melittophilous and ornithophilous characters, looking more melittophilous, but variable in corolla tube length with a relatively large volume of nectar. —P. *Salvia eremostachya* flowers with melittophilous, psychophilous, and ornithophilous characters. —Q. *Salvia greatae* flower with melittophilous and psychophilous characters. Scale bars: A, B, E, H, J–L, O, P, = 1 cm; C, D, F, G, M, N, Q = 0.5 cm; I = 0.25 cm.

more or less fruity scent of the corolla and the calyx was detected. Nectar of medium volume was found protruding 5–11 mm into the tube.

Although several populations were studied at roadside localities in western Texas, no pollinators were seen. Nevertheless, we deduce from the floral traits and proportions, tube dimensions, and landing platform that butterflies and/or long-tongued flies are the pollinators of the species.

REMAINING SPECIES

The remaining New World *Salvia* species (Appendix 2) share characters with species of different groups and thus allow different pollinator guilds access to nectar (see Table 2) or are too little known to be characterized sufficiently.

Species probably pollinated by bees and birds. *Salvia purpurea* Cav. (*Salvia* subg. *Calosphace*; Table 2) has highly variable flowers with different corolla colors, flower sizes, and proportions of tube to lower lip length (sometimes even within one individual). Long-tubed flowers with relatively short lower lips allow birds access to the nectar, but exclude bees. Flowers with longer lower lips, offering a better landing platform for bees, may be pollinated by both birds and bees. Indeed, field observations in Mexico confirmed that hummingbirds (hovering and perching) and bees visit the flowers, being dusted with pollen. Bees were also found as nectar and pollen thieves and different species of butterflies and hawkmoths stole nectar. Additonally, studies in Mexico showed that the activity of flower visitors varied. At some places hummingbirds were more frequent (Guadalajara); at other localities bees were more abundant (Xalapa).

The yellow flowers of *Salvia aspera* M. Martens & Galeotti (*Salvia* subg. *Calosphace*; Fig. 6L; Table 2) also vary in length. Although the larger flowers with a relatively large volume of nectar with medium sugar concentration may attract birds, the smaller ones may also allow bees access to nectar. Their lower lips are relatively narrow, but stable enough to present a landing platform for bees.

The dark violet corolla of *Salvia concolor* Lamb. ex Benth. (*Salvia* subg. *Calosphace*; Fig. 6K; Table 2) offers a large landing platform for bees at its lower lip. However, the long corolla tube probably excludes bees from nectar. The medium amount of nectar with its relatively low sugar concentration also indicates bird pollination. We assume that bees might reach the nectar in short-tubed flowers, but are excluded in longer ones.

Salvia mexicana L. (*Salvia* subg. *Calosphace*; Table 2) is a quite variable species with two varieties, *S. mexicana* var. *minor* Benth. and *S. mexicana* var. *major* Benth. In general, the varieties considerably differ in corolla size, in the proportion of tube to lower lip length, and in the lower lip position. Additionally, these characters and the corolla color differ within the varieties and overlap. The large flowers in both varieties and the flowers with a relatively short lower lip in comparison to the flower tube are clearly ornithophilous as they exclude bees from nectar. Smaller flowers, especially those with long lower lips, are thought to be intermediate and/or pollinated by bees. Nectar data of the examined individuals in both varieties might be rather attractive to birds. Indeed, at the lighter violet flowers of *S. mexicana* var. *major*, hummingbirds were observed visiting the flowers, while bees stole nectar.

The following three species have small- to medium-sized corolla tubes and large lower lips that clearly allow bees access to nectar. The blue *Salvia scutellarioides* Kunth (*Salvia* subg. *Calosphace*; Table 2) with white nectar guides on the lower lips and rather short corolla tubes has a medium volume of nectar with a relatively low sugar concentration. Furthermore, flowers have exposed thecae that might not be touched by bees. *Salvia discolor* Kunth (*Salvia* subg. *Calosphace*; Table 2), with a dark violet (almost black) corolla contrasting to the whitish green calyx, corresponds to the bee-pollinated flowers in its large lower lip, short- to medium-sized tube, and nectar of high sugar concentration. However, nectar guides are lacking and the large volume of nectar might also attract birds. *Salvia retinervia* Briq. (*Salvia* subg. *Calosphace*; Table 2; Fig. 6O), with a dark violet tube of variable length, also has a relatively large volume of nectar, which might be attractive to birds. In Bolivia, large bees were observed to pollinate the species, whereas other bee species stole nectar.

Species probably pollinated by birds and butterflies/long-tongued flies. In contrast to the above-mentioned species, *Salvia mohavensis* Greene (Fig. 6M) and *S. clevelandii* (A. Gray) Greene (both *Salvia* sect. *Audibertia*; both Table 2) exclude bees due to their long and narrow corolla tubes and exserted thecae. Their medium volume of nectar with a medium to low sugar concentration corresponds to this finding.

The blue to blue-violet flowers of *Salvia clevelandii* have a strong sweet scent that might be attractive to butterflies. Although butterflies were indeed observed at the flowers (Rancho Santa Ana Botanic

Table 2. Characteristics of selected *Salvia* species with intermediate characters.

Salvia spp.	Corolla length, mm	Corolla tube length, mm	Lower lip length, mm	Lower lip position*	Flower shape*
purpurea Cav.	(12)19–36	(9)12–21	(3)7–11	a, rarely d	b
aspera M. Martens & Galeotti	23–40	13–26	13–17	a, rarely d	b
concolor Lamb. ex Benth.	22–34	14–27	8–10	a	b
mexicana L.	var. *major*: 28–49; var. *minor*: 15–29	var. *major*: 18–29; var. *minor*: 11–20	var. *major*: 9–17; var. *minor*: 5–11	var. *major*: a or d; var. *minor*: a	b
scutellarioides Kunth	16–25	10–16	8–12	a	b
discolor Kunth	20–30	13–19	8–16	a	b
retinervia Briq.	21–30	12–20	11–14	a	b
clevelandii (A. Gray) Greene	18–29	12–20	4–6	a, ah	± t
mohavensis Greene	moh.: 19–30; Pinacate form: 17–25	moh.: functional tube: 16–25; Pinacate form: 16–22	moh.: 4–7; Pinacate form: (3)4–5	moh.: d; Pinacate form: ah, lc	moh.: s; Pinacate form: t
eremostachya Jeps.	18–25	12–17	9–13	a	± t
greatae Brandegee	13–20	8–13	3–7	a	t

Table 2. Extended.

Salvia spp.	Exposition of thecae from upper lip, mm	Corolla color*	Nectar guides on corolla	Nectar concentration, %*	Nectar volume, µl*
purpurea Cav.	0	Pi to Pu or Vi C20–70 M50–99 S00–10, rarely liPi C00 M10 S00 or Wh C00 M00 S00	absent		
aspera M. Martens & Galeotti	0	Ye Y70–80 M00–05 S00	absent	28.8 ± 1.3 (24.3–31.5), n = 29	l
concolor Lamb. ex Benth.	0	daVi C99 M95 S00	absent	21.2 ± 2.8 (15.2–25.8), n = 33	m
mexicana L.	0	var. *major* and var. *minor*: daVi C90–99 M80–90 S00–20, var. *major*: sometimes also meVi and liVi C60–90 M50–80 S00 or whitish C00–10 M00–10 S00; calyx blackish to green and yellowish	absent	var. *major*: 18.7 ± 5 (9–26), n = 34; var. *minor*: 27.3 ± 3.1 (20.5–36), n = 61	var. *major*: mostly l; var. *minor*: m to l
scutellarioides Kunth	(4–7)	Bl C99 M80 S00	white	23.7 ± 2.1 (19–34.4), n = 59	4.5 ± 1.2 (2–7.5), n = 29; m
discolor Kunth	0	daVi (almost black) C99 M90 S80–90; calyx whitish light green	absent	> 40 (19.4 to > 62), n = 55	21.3 ± 7.7 (11–44), n = 15; l
retinervia Briq.	0	daVi C99 M90 S00	absent		l
clevelandii (A. Gray) Greene	5–9	Bl to BlVi C70–90 M60–80 S00	absent	26 ± 2.4 (20.2–31.6), n = 37	m
mohavensis Greene	8–13 (both forms)	moh.: liBl C20–40(50) M10–30(40) S00, bracts Wh/whitish, rarely with paVi/yellowish; Pinacate form: liPi/Vi/Lav C10–30 M20–50 S00, lips at their inner part C50 M70 S00, bracts green	absent (both forms)	moh.: 19 ± 6.4 (8–37). n = 32	moh.: m
eremostachya Jeps.	4–6	(pale) ViPi to almost Wh C10 M10 S00, C60 M60 S00	absent	17.4 ± 2.9 (14.5–21), n = 6	m
greatae Brandegee	0–3	Pi-Lav (lower lip: C40–50 M60–90, tube: C10–20 M20–40 S00)	sometimes pale whitish		s

Table 2. Extended.

Salvia spp.	Flower scent	Observations of hummingbirds	Reports of hummingbirds	Observations of insects	Reports of insects
purpurea Cav.	no	*Selasphorus rufus*, *Hylocharis leucotis*, *Archilochus* cf. *colubris*, *Cynanthus latirostris* (field, Mexico; hovering and perching)	visited by *Doricha eliza* (Ortiz-Pulido et al., 2002)	visited by various bee species dusted with pollen (e.g., cf. *Eulaema*), visited by other bees, different butterflies, and hawkmoths stealing nectar (field, Mexico)	visited by 5 bee species robbing nectar (Dieringer et al., 1991); visited by *Euglossa atroveneta* drinking nectar (Ramírez & Martínez, 1998)
aspera M. Martens & Galeotti	no				pollinated by bees (possibly only concluded because of corolla color; Ramamoorthy & Elliott, 1998)
concolor Lamb. ex Benth.	no		visited and apparently pollinated by hummingbirds (*Beaman 2068*, MEXU)		
mexicana L.	no	var. *major*: unidentified hummingbirds (field, Mexico; hovering)	both vatieties: visited/ pollinated by hummingbirds (Wagner, 1946; Des Granges, 1979; Geisfield, 1987; Arizmendi et al., 1996; Lara & Ornelas, 2001)	*major*: visited by bees stealing nectar (field, Mexico)	*major* and *minor*: pollinated by *Deltoptila elefas*, other bee species as robbers (Dieringer et al., 1991); bumble bees as pollinators and robbers (Arizmendi et al., 2007); *major*: visited by *Anthophora* sp. (Reisfield, 1987); *minor*: visited by *Bombus nigrodorsalis* robbing nectar (Reisfield, 1987); rarely legitimate bee visits (compared to hummingbirds; C. Lara, pers. comm.)
scutellarioides Kunth	no				visited by *Bombus atrata* (Rasmussen, 2004)
discolor Kunth	no				
retinervia Briq.	no			visited/pollinated by large bees, visited by other bees stealing nectar and pollen (field, Bolivia)	

Table 2. Extended. Continued.

Salvia spp.	Flower scent	Observations of hummingbirds	Reports of hummingbirds	Observations of insects	Reports of insects
clevelandii (A. Gray) Greene	sweet	*Archilochus alexandri* (cult.: Rancho Santa Ana Botanic Garden; hovering)	visited/pollinated by hummingbirds (Cox, 1981; B. O'Brien, pers. comm.)	visited by different bee species robbing nectar (e.g., *Xylocopa* sp., *Apis mellifera*), visited by butterflies (cult.: Rancho Santa Ana Botanic Garden)	visited by hawkmoths (*Hemaris thysbe*), nectar-robbing bees piercing corolla (*Xylocopa* sp., rarely touching reproductive organs), nectar-stealing small bees using these holes (*Apis mellifera*, *Megachile* sp.) (Cox, 1981)
mohavensis Greene	no (both forms)	moh.: hummingbird (cult.: Rancho Santa Ana Botanic Garden; hovering)	Pinacate form: visited by hummingbirds (A. Sanders, pers. comm.)		moh.: visited by long-tongued flies (B. O'Brien & P. Wilson, pers. comm.; Fenster et al., 2004)
eremostachya Jeps.	no		at least occasionally pollinated by hummingbirds (E. Jones, pers. comm.)		
greatae Brandegee	sweetish	hummingbird (cult.: Rancho Santa Ana Botanic Garden; hovering)		visited by a fly (field, U.S.A.)	

* Refers to the following classification (see Methods): **Lower lip position:** d = deflexed, a = antrorse (ah = ± horizontal, not flexed), lc = lower and upper lips close to each other. **Flower shape:** b = bilabiate, t = tubular, s = Stielteller. **Color:** Bl = blue, Lav = lavender, Pi = pink, liPi = light pink, Pu = purple, Vi = violet, Wh = white, Ye = yellow; da = dark, li = light, pa = pale, me = medium. CMYK after Küppers (1999; C: cyan, M: magenta, Y: yellow, K [here S]: black). **Nectar concentration** (average, SD, range). **Nectar volume** (average, SD, range): s = small (< 3 µl), m = medium (about 3–10 µl), l = large (> 10 µl).

Garden), they were not the exclusive visitors as hovering hummingbirds also visited and probably pollinated the flowers. Nectar-robbing bees of different species pierced the flowers at their base.

Salvia mohavensis, studied at different localities in California, has bracts that are partly white or whitish, rarely with pale violet or yellowish areas. The corollas are light blue (Fig. 6M). Their lips form a more or less discoidal and widespread arranged disc, making the flowers only somewhat zygomorphic. Together with the corolla tube this lip formation results in the typical Stielteller shape of the flowers. In the Fullerton Arboretum, hummingbirds were observed visiting the flowers. However, cultivated plants in a private garden in Tucson (M. Dimmitt), originating from an isolated occurrence of the species in northern Mexico (the Pinacate region), have different flowers. The bracts are green and the corolla light pink to violet to lavender. The flowers differ in floral tube width and lip orientation, giving them a tubular shape that lacks a landing platform, and thus are more likely to be visited and pollinated by birds (Fig. 6N).

Species probably pollinated by bees, butterflies/long-tongued flies, and birds. The flowers of *Salvia eremostachya* Jeps. (*Salvia* sect. *Audibertia*, Fig. 6P; Table 2) are (pale) violet-pink to almost white. Their short to medium-sized and relatively narrow corolla tubes and large lower lips allow bees, birds, and butterflies/long-tongued flies access to the nectar. However, the thecae and stigma are exserted and whether or not a visitor is a pollinator is dependent on its body proportions. The nectar of cultivated plants has a relatively low sugar concentration. This might be less attractive for bees, but accepted by birds or butterflies/long-tongued flies.

Species probably pollinated by bees and butterflies/long-tongued flies. The pinkish lavender flowers of *Salvia greatae* Brandegee (*Salvia* sect. *Echinosphace*, Fig. 6Q; Table 2) are small and tubular. They vary in tube length and the relative proportions of tube and lower lips. Bees are assumed to be pollinators of flowers with a shorter tube length, while butterflies or long-tongued flies may be pollinators of the longer-tubed flowers. Once a hummingbird was observed at the flowers (Rancho Santa Ana Botanic Garden), as well as a fly (field, California, U.S.A.), but it is not clear whether they indeed pollinated the flowers. Due to the low volume of nectar and the sweetish scent, bird pollination appears unlikely. The scent might be rather attractive to bees or butterflies.

Discussion

Pollination Syndromes in the New World *Salvia* Species

There are numerous genera with species adapted to different pollinator groups (birds, bees, and others; e.g., Kay et al., 2005; F. Pérez et al., 2006; Wilson et al., 2006), but a survey of such a large number of species has never been done (426 species of *Erica* L. [Rebelo et al., 1985]; 208 taxa including subspecies or varieties of *Pelargonium* L'Hér. [Struck, 1997]). In the present study our attempt to group all of the 602 New World *Salvia* species according to pollinator groups/pollination syndromes was successful. The great majority (almost 90%) of the species could be identified as having either bird-pollinated or bee-pollinated flowers. Although the correspondence between our grouping and the traditionally distinguished pollination syndromes is high, our approach is empirical. We added some new essential data, not only by asking whether a flower would fit to a certain pollinator, but also by testing which visitors might be excluded from the process of pollen transfer. Consequently, our description of ornithophilous species differs from previously existing ones.

Ornithophily: An update of phenotypic characters and geographic distribution in bird-pollinated sages. According to our grouping, about one third of the New World sages are ornithophilous, showing a high diversity of floral characters. Referring to all *Salvia* species (worldwide), about 20% appear to be bird pollinated. Although many of the sages traditionally seen as bird pollinated correspond to our grouping (e.g., Delpino, 1868–1874; Trelease, 1881, 1882; Gams, 1927; Zalewska, 1928; Himmelbaur & Stibal, 1932, 1933, 1934; Reisfield, 1987; Ramamoorthy & Elliott, 1998; Torke, 2000; Walker & Elisens, 2001), there are also disagreements. *Salvia carduacea*, for instance, was classified as an ornithophilous species by Zalewska (1928; see also Pickens, 1936). Although hummingbirds occasionally visit this species, they might never or only accidentally contact the reproductive organs (Visco & Capon, 1970; Read, 1983). Sometimes a few species of moths and butterflies were noticed at the flowers. However, it is unclear whether they contacted the pollen sacs and stigma, and pollen was never found on their bodies (see also Visco & Capon, 1970; Read, 1983). On the contrary, several species of bees were observed to land on the lower lip of the sweet-scented flowers. While drinking nectar or collecting pollen, the bees often came into contact with the reproductive organs and their bodies were dusted

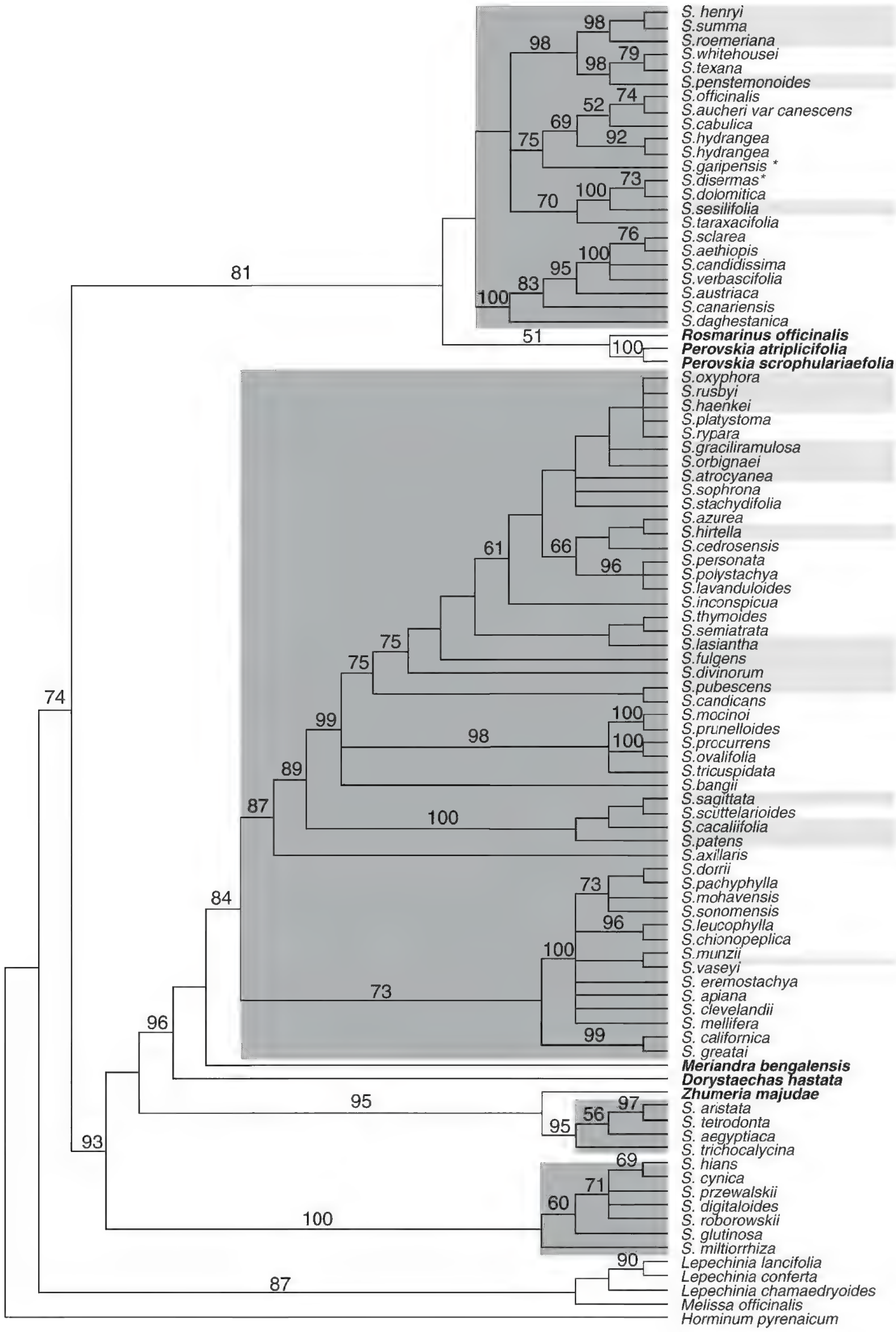

Figure 7. Phylogenetic relationships in *Salvia* s.l. (dark gray) with bird-pollinated species indicated (light gray). The phylogeny is based on Walker and Sytsma (2007). The gray line between *S. munzii* and *S. vaseyi* indicates the position of *S. spathacea* within *Salvia* sect. *Audibertia* (see Walker et al., 2004).

with pollen (Visco & Capon, 1970; Read, 1983; this study). Faegri and van der Pijl (1971) assumed *S. lasiantha* to be myiophilous without giving reasons. Although the species has relatively short corolla tubes, it appears ornithophilous to us, with its usually deflexed or reflexed lower lips and exserted thecae (Wester & Claßen-Bockhoff, 2007). *Salvia cacaliifolia* Benth. was listed as melittophilous by Cruden (1972), but hummingbirds were observed at the flowers while getting dusted with pollen (Wester & Claßen-Bockhoff, 2007; see also Skutch, 1940). The flowers have short lower lips with front margins that are often oriented upward, making landing difficult for insects. It is unlikely that bees are pollinators as they would hardly touch the exposed reproductive organs. Trelease (1882) discussed *S. heerii* Regel as being ornithophilous and psychophilous. According to Trelease, the species' long corolla tube and small lower lip prevent bees from landing on the flowers and from reaching the nectar, while the floral form and the large amount of nectar point to birds as a likely pollinator. He also mentioned a narrow passage beneath the connectives and white nectar guides as being suggestive of psychophily. We do not agree with this because the reduced lower lip does not offer a suitable landing platform for butterflies; we regard the species as typically ornithophilous. We also do not share the opinion of Faegri and van der Pijl (1971: 179) that the flowers in *S. coccinea* are only "semi-ornithophilous" because of their labiate shape. Correspondingly, we disagree with Reisfield (1987: 262, 279), who mentioned many ornithophilous species with bilabiate flowers (e.g., *S. fulgens* Cav. and *S. patens*) as being in a "transition phase" between melittophily and ornithophily. Additionally, contrary to the common view that ornithophilous flowers are characterized by stiff corollas, we also found weaker flowers to be bird pollinated, at least in species with short- to medium-sized flowers. This fits our observations that hummingbirds handle the flowers without damaging them (see also Snow & Snow, 1980). Stiff corollas are not absolutely needed to protect the flowers against visiting birds and robbing birds or bees, as stated by Proctor et al. (1996). Instead, these animals are also able to pierce strengthened corollas (e.g., *S. grewiifolia* S. Moore and *S. leucantha*, Wester & Claßen-Bockhoff, 2007). We conclude that stiff corollas stabilize the flowers rather than protect them from birds.

In addition to corolla shape and stability, corolla color of the ornithophilous sages also differs from what has been suggested by other authors. According to Baumberger (1987), 52% of the ornithophilous angiosperms have multicolored corollas (see also Porsch, 1924; Faegri & van der Pijl, 1971) (including nectar guides), but in sages the corolla is usually unicolored; it only contrasts with the calyx or leaves.

The distribution of ornithophilous New World sages does correspond to that of hummingbirds. In regions with a high number of ornithophilous *Salvia* species, hummingbirds show their highest species number and diversity (Schuchmann, 1999; see also Reisfield, 1987). Furthermore, as do bird-pollinated plants in general, ornithophilous sages appear primarily at higher altitudes (Cruden, 1972; Feinsinger, 1983; Reisfield, 1987; Kay et al., 2005). This corresponds to the equally high abundance of hummingbirds at similar altitudes (Cruden, 1972; Schuchmann, 1999; Altshuler et al., 2004). The interdependence between bird-pollinated flowers and hummingbirds is also supported by a comparison of floral tube lengths (of ornithophilous sages and ornithophilous angiosperms in general) with bill lengths in hummingbirds. For example, both the range of bill lengths and tube lengths in general broadens with lower latitude (Baumberger, 1987; Schuchmann, 1999).

Melittophily: Barriers in flowers as adaptation to bees. While ornithophilous flowers definitely exclude bees, bee-pollinated flowers do not exclude birds. However, birds are more attracted by ornithophilous species because their flowers, for example, produce larger quantities of nectar (see Faegri & van der Pijl, 1971; Stiles, 1981; Rodríguez-Gironés & Santamaría, 2004).

The examined species of the bee-pollinated sages differ from the general picture of bee-pollinated flowers (Vogel, 1954) in nearly lacking a definite petal scent (exceptions in *Salvia* sections *Audibertia* and *Echinosphace*). They share this character with many other Lamiaceae, which instead produce scent in their sepals and vegetative leaves. This scent is assumed to be used for pollination in insect-pollinated species, while a typical melittophilous scent is largely lacking (Mattern & Vogel, 1994).

There are two unusual features related to floral organization worth noting in bee-pollinated species. First, more or less concealed or closed floral entrances due to connivent corolla lips appear in some species (e.g., in *Salvia betonica*, *S. lavanduloides*), resembling those in the tribe Antirrhineae Chav. (Plantaginaceae Juss.), for example. This blocking of the entrance protects pollen and forces the bees to handle the flower with physical force (see Westerkamp & Claßen-Bockhoff, 2007). Also, there is often one additional staminal barrier in the flowers narrowing the entrance. As Claßen-Bockhoff et al.

(2004a) found, this barrier may either be the sterile thecae (*S. uliginosa*) of the two adjacent stamens or a ventral outgrowth of their sterile connective arms (*S. rypara*, Fig. 6D), illustrating that different morphological structures result in the same functional constructions in the flower. Besides blocking the flower entrance, the large barrier contributes to the release of the lever mechanism as the bees encounter this barrier in their search for nectar (see also Reisfield, 1987). As the majority of the New World *Salvia* species belong to subgenus *Calosphace*, they have straight posterior lever arms that reach far behind the flower entrance. By producing ventral protrusions, a lever apparatus results that parallels the form of the curved levers, typical for many bee-pollinated species from the Old World (see also Hildebrand, 1865; Ogle, 1869; Correns, 1891; Himmelbaur & Stibal, 1932, 1933, 1934). Perhaps bee-pollinated flowers need such a barrier to enable the bees to release the lever mechanism. In contrast, such an auxiliary construction is not needed in bird-pollinated flowers as birds are able to touch each kind of abutment with their long bills.

Indications of psychophily in Salvia. The genus *Salvia* encompasses only a few species assumed to be psychophilous, e.g., *S. scabra* L. f. in South Africa (long-tongued flies assumed by Potgieter & Edwards, 2001) or *S. nanchuanensis* Y. Z. Sun in China (Wester, unpublished). Until now, no observations of flower-pollinator interactions exist in these species. This is also true for *S. whitehousei* (Fig. 6J), which we assume to be a further psychophilous species in the New World, with butterflies or psychoid insects (long-tongued flies) as pollinators. This species is only known from Texas and Coahuila (Mexico) and is little known. The upper lip does not have the typical hooded or galeate shape of most of the sages including other representatives of *Salvia* sect. *Salviastrum* (e.g., *S. texana*, Fig. 6B, C) and most of the *Salvia* species in subgenus *Calosphace*, and as incorrectly illustrated in the only published description by Whitehouse (1949). Instead, the lips of *S. whitehousei* spread at a right angle to the long tube and thus the flower forms a Stielteller flower sensu Vogel (1954), being characteristic for psychophilous flowers.

Intermediates or not clearly assignable species. We found "intermediate flowers" not clearly belonging to a specific pollination syndrome. They could not be grouped because of fragmentary or conflicting descriptions or because they share characters of several syndromes (for instance, bee-pollinated and bird-pollinated flowers). Because of evolutionary transitions, we expect that not all species can be classified into pollination syndromes. They illustrate natural variation and should not be taken as an argument against the validity of pollination syndromes.

One species that provides an example of conflicting or missing data is *Salvia purpurea*, which is highly variable in color, size, and proportions. Dependent on the locality and time of observation, either hummingbirds, butterflies, or bees are reported to be more abundant (C. González, M. Ordano & A. Luis-Martínez, pers. comm.). Different visitor groups were also found in *S. clevelandii*, which is reported to be often visited and pollinated by hummingbirds and also by small hawkmoths (Cox, 1981; B. O'Brien, pers. comm.). The yellow flowers of *S. aspera* are mentioned to be pollinated by bees (Ramamoorthy & Elliott, 1998), but it is possible that this conclusion refers to the yellow color taken as a typical melittophilous trait. Instead, bird-pollinated species also have yellow flowers.

Difficulties are also caused by taxonomic conflicts. Some taxa may be recognized as synonyms or some species may include highly variable subspecies or varieties (*Salvia arenaria* A. St.-Hil. ex Benth., *S. amethystina* Sm., *S. carnea* Kunth, *S. mexicana*; see also Appendix 3). *Salvia carnea*, for instance, includes formerly separate species that vary in flower size and color. The morphs range from ornithophilous (*S. carnea* var. *punicans* (Epling) J. R. I. Wood & Harley) to melittophilous (sensu *S. gracilis* Benth.), forming a continuum with other taxa like a "ring of races" (Reisfield, 1987: 278). The appearance of different morphs within a species complicates their grouping. *Salvia mohavensis*, for instance, is distributed in the southwestern United States and northern Mexico (Neisess, 1983; A. Sanders, pers. comm.). The widespread "normal" light blue Stielteller flowers combine ornithophilous and psychophilous characters and are observed to be visited by hummingbirds and long-tongued flies (Fenster et al., 2004; B. O'Brien & P. Wilson, pers. comm.), with the latter classified as psychoid insects. Individuals of *S. mohavensis* in northern Mexico, isolated by 300 km, have flowers with a rather ornithophilous form (broader corolla tube, lip orientation, color) and are reported to be visited by hummingbirds (A. Sanders, pers. comm.). If gene flow is disrupted between these different morphs, subspecies or even new species may evolve (cf. Johnson, 1997).

Morphological intermediates sharing characters of two or three pollination syndromes can be interpreted in different ways. One interpretation is that the

classification is inappropriately narrow and excludes less typical representatives from a syndrome. Another possible interpretation is that the intermediates represent momentary transitional stages from one syndrome to the other, following a strong unidirectional selection pressure (see also Reisfield, 1987; for other genera, see, e.g., Baker, 1963; Stebbins, 1974; Macior, 1986; Sazima et al., 1994; Manning & Goldblatt, 2005; Wilson et al., 2006). These intermediates might be attractive for different groups at the same time, for example, for bees (e.g., landing platform, short corolla tube) and birds (e.g., a larger volume of nectar) (e.g., F. Pérez et al., 2006; Wilson et al., 2006; see also Hardy, 1954; Thomson et al., 2000; Thomson, 2003).

Given the assumed shift between different pollinator groups and ecologic constraints, intermediate stages among clearly adapted flowers should be expected. This is especially true for the young and evolutionarily unstable *Salvia* subg. *Calosphace* and *Salvia* sect. *Audibertia*, which include many endemics and highly variable species (*Salvia* subg. *Calosphace*, Reisfield, 1987) and hybrids (especially section *Audibertia*; Emboden, 1971; Neisess, 1983). However, the limited number of intermediate flowers in *Salvia* indicates a strong selection pressure against the presence of more than one dominant pollinator group.

PARALLEL EVOLUTION OF POLLINATION SYNDROMES IN THE GENUS *SALVIA*

Because bee-pollinated and bird-pollinated flowers are found in different lineages in the Old and New World and differ in their floral morphologies, their parallel evolution is obvious (see also Himmelbaur & Stibal, 1932, 1933, 1934; Grant & Grant, 1965; Baumberger, 1987; Reisfield, 1987; Wester & Claßen-Bockhoff, 2006b, 2007). This has also been confirmed by the phylogenetic studies of Walker and Sytsma (2007). Referring our results to their phylogenetic tree (Fig. 7; Walker & Sytsma, 2007: 383), ornithophilous species appear in two of their three clades. Following parsimony in their clade I (Walker & Sytsma, 2007), the New World taxa (*Salvia* sect. *Heterosphace*, *Salvia* sect. *Salviastrum*, and *S. pentstemonoides*) show two parallel shifts from melittophily to ornithophily and one from melittophily to psychophily (see also Walker et al., 2004: 1118). A further shift from melittophily to ornithophily in clade I is found for the Madagascan *S. sessilifolia* Baker (see also Wester & Claßen-Bockhoff, 2006b). In their clade II, shifts from melittophily to ornithophily happened at least twice in the New World *Salvia* subg. *Calosphace* and at least once in the New World *Salvia* sect. *Audibertia* (for *S. spathacea*, see Walker et al., 2004). *Salvia* thus corresponds to genera such as *Aquilegia* L., *Costus* L., *Mimulus* L., and *Penstemon* Schmidel (Beardsley et al., 2003; Castellanos et al., 2004; Kay et al., 2005; Wilson et al., 2006; Whittall & Hodges, 2007), in which similar repeated shifts from entomophilous to ornithophilous species have been documented. In view of the many species in *Salvia*, with the ongoing phylogenetic research in New World species (Dos Santos, pers. comm.; Jenks, pers. comm.; Walker, pers., comm.) and hopefully more extended field studies, the genus could represent an adequate model system to investigate the evolution of ornithophily in more depth.

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APPENDIX 1. List of sources used for the 602 *Salvia* species. Sources are listed in this order: the literature, herbarium specimens, plants studied in the field (wild), and in cultivation (cult.); square brackets indicate that only pickled flowers were available. Asterisks follow type specimens.

S. acerifolia B. L. Turner: Turner, 2008a; *Cowan 5646** (TEX-LL). ***S. acuminata*** Ruiz & Pav.: Ruiz & Pavon, 1798; Epling, 1939; *Macbride 3661* (F); *Weberbauer 6699* (GH). ***S. adenophora*** Fernald: Epling, 1939; dos Santos, 1991; *M. Crone 7* (MJG, cult.); *Nelson 2093**, *2093a** (US). ***S. aequidistans*** Fernald: Epling, 1939; *Rose 1609** (NY). ***S. agnes*** Epling: Epling, 1939; *Mexia 1582a** (C, NY). ***S. alamosana*** Rose: Epling, 1939; *Palmer 345** (US). ***S. alariformis*** L. O. Williams: Standley & Williams, 1973; *Williams & Molina 11459** (GH). ***S. alata*** Epling: Epling, 1960; Epling & Játiva, 1963; *Angulo 1684** (HUT, UC-JEPS); *Sagástegui 7691* (GH). ***S. alba*** J. R. I. Wood: Wood, 2007. ***S. albiflora*** M. Martens & Galeotti: Standley & Williams, 1973; Dieringer et al., 1991; Pool, 2001. ***S. albocaerulea*** Linden: Epling, 1939; *Ramos Marchena s.n.* (B). ***S. alborosea*** Epling & Játiva: Epling & Játiva, 1966; Sagástegui et al., 2003; *Hart 1533* (K); *Lezama & Veneros 15557* (K); *Llatas Quiroz 2141* (F); *López et al. 3724** (UC-JEPS); *Sagástegui 15910* (TEX-LL). ***S. aliciae*** E. P. Santos: dos Santos, 1993; *S. Vogel 1965/613* (WU). ***S. altimitrata*** Epling: Epling, 1939; *Goldman 823** (US). ***S. altissima*** Pohl: Epling & Toledo, 1943; *Pohl 1718* (K). ***S. alvajaca*** Oerst.: Standley & Williams, 1973; Pool, 2001; *Allen 1355** (MO, US). ***S. amarissima*** Ortega: Epling, 1939. ***S. amethystina*** Sm.: Epling, 1939, 1941; Wood & Harley, 1989; Fernández Alonso, 1995a; *Fernández Alonso et al. 11688** (COL); *Haught 6192** (US); *Humboldt & Bonpland s.n.** (P); *Wood 5031** (COL). ***S. amissa*** Epling: Epling, 1939; *Pringle 1001** (NY). ***S. ampelophylla*** Epling: Epling, 1939; Reisfield, 1987; Wood & Harley, 1989; Fernández Alonso, 2003; see also Appendix 3. ***S. amplifrons*** Briq.: Epling, 1939; Wood, 2007; *S. Vogel 1965/500* (WU); *P. Wester 141* (LPB, MJG, wild, cult.). ***S. anastomosans*** Ramamoorthy: Ramamoorthy, 1984c; Dieringer et al., 1991. ***S. anguicoma*** Epling: Epling, 1947; *Steyermark 55830** (UC-JEPS). ***S. angulata*** Benth.: Epling, 1939; *Smith 1370** (NY, TEX-LL). ***S. angustiarum*** Epling: Fernald, 1900; Epling, 1939; Reisfield, 1987; *Palmer 184** (GH, MO, NY, P, US); *Pringle 9377* (B). ***S. apiana*** Jeps.: Pickens, 1929; Epling, 1938; Grant & Grant, 1964; Neisess, 1983; Reisfield, 1987; *P. Wester 396*, *410*, *455* (MJG, wild), *411* (MJG, UCR, wild), *597* (MJG, cult.). ***S. apparicii*** Brade & Barb. Per.: Brade & Barbosa, 1946. ***S. aratocensis*** (J. R. I. Wood & Harley) Fern. Alonso: Wood & Harley, 1989; Fernández-Alonso, 2003; see also Appendix 3; *Wood 5052** (COL). ***S. arborescens*** Urb. & Ekman: Epling, 1939; Liogier, 1994. ***S. arbuscula*** Fernald: Epling, 1939; *Langlassé 767** (G, GH, K, P). ***S. arduinervis*** Urb. & Ekman: Torke, 2000; *Ekman H-3168/b** (GH, K, NY). ***S. arenaria*** A. St.-Hil. ex Benth.: Epling, 1939; Epling & Toledo, 1943; Epling & Mathias, 1957; Sazima et al., 1996; Buzato et al., 2000; *Dusén s.n.* (US); *Irwin 2780* (NY); *S. Vogel 1965/751*, *1965/688* (WU). ***S. areolata*** Epling: Epling, 1944, 1947; *Steyermark 50338** (UC-JEPS). ***S. aridicola*** Briq.: Epling, 1939; dos Santos, 1996; *Hassler 5227** (NY). ***S. arizonica*** A. Gray: Epling, 1939. ***S. arthrocoma*** Fernald: Epling, 1939; *Pringle 8940** (L). ***S. articulata*** Epling: Epling, 1939; Epling & Toledo, 1943; dos Santos, 1991; *W. Hoehne s.n.* (K); *Mosén 1922** (S); *Krapovickas & Cristóbal 35441* (K); *Regnell I 312* (K); *S. Vogel 1965/784* (WU). ***S. aspera*** M. Martens & Galeotti: Epling, 1939; *Pringle 6240* (P); *P. Wester 257* (MEXU, MJG, wild), *261* (MJG, wild), *546* (MJG, cult.). ***S. assurgens*** Kunth: Epling, 1939; *Humboldt & Bonpland s.n.** (P); *Pringle 4150* (F). ***S. atrocalyx*** Epling: Epling, 1939; *Killip 24401** (F, GH, NY, US). ***S. atrocaulis*** Fernald: Epling, 1939; *Pringle 8887** (C, GH, K, P, S, US). ***S. atrocyanea*** Epling: Epling, 1939; Legname, 1962; Pontiroli, 1993; Wester & Claßen-Bockhoff, 2007; Wood, 2007; *P. Wester 3* (K, LPB, MJG, wild), *5–7* (MJG, wild), *8* (MJG, wild, cult.). ***S. atropaenulata*** Epling: Epling, 1939, 1940a; *Mexia 9056** (B, GH, MO, NY, US). ***S. austromelissodora*** Epling & Játiva: Epling & Játiva, 1966. ***S. axillaris*** Moç. & Sessé ex Benth.: Epling, 1939; Reisfield, 1987; Turner, 1996c; Ramamoorthy, 2001; *García 1168** (TEX-LL), *Pringle 6905* (MEXU); *P. Wester 269* (MJG, wild). ***S. axilliflora*** Epling: Epling, 1939; Steyermark & Huber, 1978; *Eggers 13414** (C). ***S. ayavacensis*** Kunth: Kunth, 1817; Epling, 1937, 1939; Macbride, 1960; *Weberbauer 6399** (F, GH). ***S. azurea*** Michx. ex Lam.: Epling, 1939; Peterson, 1978; *Lindheimer 145** (NY).

S. bahorucona Urb. & Ekman: Torke, 2000. ***S. balaustina*** Pohl: Epling, 1939; dos Santos, 1991; Buzato et al., 2000; *Buzato & Sazima 26.293* (K). ***S. ballotiflora*** Benth.: Epling, 1939; *Palmer 717* (P); *Wright 1524* (NY). ***S. benthamiana*** Gardner: Epling, 1939; dos Santos, 1991; *Gardner 580** (G, K, NY, UC-JEPS, US). ***S. betonica*** Schult.: Epling, 1939; *M. Crone 23* (MJG); *P. Wester* [*184*] (MJG, wild); *Humboldt s.n.* (B). ***S. betulifolia*** Epling: Epling, 1941; Ahlenslager, 1984; Van Devender et al., 2004; *Palmer 477** (MO, NY); *Reveal 3037** (MO, NY, TEX-LL, US). ***S. biserrata*** M. Martens & Galeotti: Fernald, 1900; Epling, 1939; Reisfield, 1987; *Galeotti 684** (P). ***S. blepharophylla*** Brandegee ex Epling: Epling, 1939; *Purpus 4950** (UC-JEPS), *5450** (MO, NY, US); *P. Wester 450* (MJG, cult.). ***S. boegei*** Ramamoorthy: Ramamoorthy, 1984c. ***S. bogotensis*** Benth.: Epling, 1939. ***S. booleana*** B. L. Turner: Turner, 1995c; *Lundell 5470* (TEX-LL). ***S. borjensis*** E. P. Santos: dos Santos, 1995, 1996. ***S. brachyloba*** Urb.: Epling, 1939; Liogier, 1994; *Ekman 9317* (K). ***S. brachyodonta*** Briq.: Epling, 1939; *Pringle 2463** (NA, NY, P). ***S. brachyphylla*** Urb.: Epling, 1939; Liogier, 1994; *Ekman 8252* (K). ***S. brandegeei*** Munz: Epling, 1938, 1940c; Neisess, 1983; *P. Wester 514*, *596* (MJG, cult.). ***S. breviflora*** Moç. & Sessé ex Benth.: Epling, 1939; Dieringer et al., 1991; *Pringle 8430** (P). ***S. brevipes*** Benth.: Epling, 1939; Crespo, 1979; dos Santos, 1996. ***S. buchananii*** Hedge: Hedge, 1963; *P. Wester 545* (MJG, cult.). ***S. buchii*** Urb.: Epling, 1939; Liogier, 1994; *Buch 658** (GH). ***S. bullulata*** Benth.: Epling, 1939; *Donnell Smith 765* (US); *Matthews 1862* (US).

S. caaguazuensis Briq.: Epling, 1939; dos Santos, 1996; *Hassler 4280** (NY). ***S. cabonii*** Urb.: Epling, 1939; Liogier, 1994. ***S. cacaliifolia*** Benth.: Epling, 1939; Skutch, 1940; Wester & Claßen-Bockhoff, 2007; *P. Wester 416*, *558* (MJG, cult.). ***S. calaminthifolia*** Vahl: Epling, 1939; Liogier, 1994. ***S. calcicola*** Harley: Harley, 1974; *Irwin 12026** (NY). ***S. californica*** Brandegee: Epling, 1938; Shreve & Wiggins, 1964; Neisess, 1983; *P. Wester 470*, *486* (MJG, cult.). ***S. calolophos*** Epling: Epling, 1939; *S. Vogel 1970/582* (WU). ***S. camarifolia*** Benth.: Epling, 1939; Wood & Harley, 1989; Fernández Alonso, 2002; *Smith 379* (K), *567** (GH, H, K, NY, P, TEX-LL, UC-JEPS); *Fernández Alonso et al. 13352**, *13785** (COL). ***S. campicola*** Briq.: Epling, 1939; dos Santos, 1996. ***S. camporum*** Epling: Epling, 1944; *Metcalf 30805** (GH). ***S. candicans*** M. Martens & Galeotti: Epling, 1939; *Pringle 6245* (P). ***S. capillosa*** Epling: Epling, 1940a, 1941; *Hinton 13020** (NY). ***S. carbonoi*** Fern. Alonso: Fernández-Alonso, 2003; *Kirkbride 2001** (COL). ***S. cardenasii*** J. R. I. Wood: Wood, 2007. ***S. cardiophylla*** Benth.: Crespo, 1979; dos Santos, 1996. ***S. carduacea*** Benth.: Epling, 1938; Visco & Capon, 1970; Read, 1983; *P. Wester 395* (MJG, wild). ***S. carnea*** Kunth: Fernald, 1900; Epling, 1939, 1940a; Standley & Williams,

1973; Wolf et al., 1976; Reisfield, 1987; Wood & Harley, 1989; Dieringer et al., 1991; Farji Brener, 1991; Ramamoorthy, 2001; *Hinton 11224** (NY, TEX-LL, US); *Humboldt & Bonpland s.n.** (P); *Pringle 8927** (L, NY, P, US); *Skutch 1971** (NY). ***S. caudata*** Epling: Epling, 1939; *Mueller 143** (GH). ***S. caymanensis*** Millsp. & Uline ex Millsp.: Epling, 1939. ***S. cedrosensis*** Greene: Epling, 1939. ***S. cerradicola*** E. P. Santos: dos Santos, 1993, 1996. ***S. chalarothyrsa*** Fernald: Epling, 1939; *Pringle 8856** (L, NY, P). ***S. chamaedryoides*** Cav.: Epling, 1939; *Pringle 6907* (P). ***S. chapadensis*** E. P. Santos & Harley: dos Santos & Harley, 2004. ***S. chapalensis*** Briq.: Epling, 1939; *Pringle 4351** (C, L, NY, TEX-LL). ***S. chazaroana*** B. L. Turner: Turner, 2009b. ***S. chiapensis*** Fernald: Epling, 1939; Cruden, 1972; *Gomez Lopez 179* (MEXU); *Nelson 3201** (US); *P. Wester 427* (MJG, cult.). ***S. chicamochae*** J. R. I. Wood & Harley: Wood & Harley, 1989; Fernández Alonso, 2003; *Wood 5134** (COL). ***S. chionopeplica*** Epling: Epling, 1940c; Shreve & Wiggins, 1964; Neisess, 1983; *Palmer 368** (NY); *Raven 125551** (K); *Reid Moran 20590* (SD); *P. Wester 467*, *485* (MJG, cult.); *Wiggins 5300** (GH, NY). ***S. chionophylla*** Fernald: Epling, 1939. ***S. cinnabarina*** M. Martens & Galeotti: Epling, 1939; Skutch, 1940; Standley & Williams, 1973; Dieringer et al., 1991; Schondube et al., 2004; Wester & Claßen-Bockhoff, 2007; *Pringle 4947** (P); *P. Wester 198*, *283*, *290*, *302* (MJG, wild), *265* (MEXU, MJG, wild). ***S. clarendonensis*** Britton: Epling, 1939; *Harris 12787** (NY). ***S. clarkcowanii*** B. L. Turner: Dieringer et al., 1991; Turner, 2008b; *Calzada 20723*, *21621* (MEXU), *Cowan 4941* (MEXU), *Torres 10810* (MEXU); *Martínez et al. 6191* (MEXU, RSA). ***S. clevelandii*** (A. Gray) Greene: Cox, 1981; Neisess, 1983; *P. Wester 515* (MJG, wild), [*406*], *487*, *560* (MJG, cult.). ***S. clinopodioides*** Kunth: Epling, 1939; Martínez & Matuda, 1984; *Humboldt & Bonpland s.n.** (P). ***S. coahuilensis*** Fernald: Epling, 1939; *Palmer 194** (NY). ***S. coccinea*** Buc'hoz ex Etl.: Epling, 1939; Grases & Ramírez, 1998; Ortiz-Pulido et al., 2002; *P. Wester 12* (LPB, MJG, wild), *237* (MEXU, MJG, wild), *299* (MJG, wild), *556* (MJG, cult.). ***S. cocuyana*** Fern. Alonso: Fernández Alonso, 1995a; *Wood 5139** (COL). ***S. codazziana*** Fern. Alonso: Fernández Alonso, 1995c; *Rangel 12336** (COL). ***S. cognata*** Urb. & Ekman: Epling, 1939; Liogier, 1994; *Ekman 5048** (GH, K, S, US). ***S. collinsii*** Donn. Sm.: Epling, 1939. ***S. colonica*** Standl. & L. O. Williams ex Klitg.: Klitgaard, 2007. ***S. columbariae*** Benth.: Epling, 1938; Visco & Capon, 1970; Neisess, 1983; Reisfield, 1987; *P. Wester 394*, *407* (MJG, wild). ***S. comayaguana*** Standl.: Epling, 1939; Pool, 2001; *Standley 55843** (US). ***S. compsostachys*** Epling: Epling, 1940a. ***S. concolor*** Lamb. ex Benth.: Epling, 1939; Ramamoorthy, 2001; *Beaman 2068* (MEXU); *P. Wester 167* (MEXU, MJG, wild, cult.). ***S. confertiflora*** Pohl: Epling, 1939; dos Santos, 2004; *P. Wester 561* (MJG, cult.). ***S. congestifolia*** Epling: Epling, 1939; Epling & Toledo, 1943. ***S. connivens*** Epling: Epling, 1939; *Pringle 3224** (P, TEX-LL). ***S. consimilis*** Epling: Epling, 1939; Epling & Toledo, 1943. ***S. consobrina*** Epling: Epling, 1960; *López 2281** (HUT, UC-JEPS); *Weberbauer 7654* (F). ***S. cordata*** Benth.: Epling, 1939; dos Santos, 1996. ***S. corrugata*** Vahl: Epling, 1939, 1941; Wood & Harley, 1989; *Hutchinson 6575* (F); *P. Wester* [*590*] (MJG, cult.). ***S. costaricensis*** Oerst.: Epling, 1939; Hedström, 1985. ***S. costata*** Epling: Epling, 1939; Wood & Harley, 1989. ***S. coulteri*** Fernald: Epling, 1939; *Coulter 1120** (K, NY). ***S. crucis*** Epling: Epling, 1939. ***S. cruckshanksii*** Benth.: Epling, 1939; *Matthews 464** (L); *Penell 14332* (F). ***S. cryptodonta*** Fernald: Epling, 1939. ***S. cuatrecasana*** Epling: Epling, 1944; Wood & Harley, 1989; Fernández Alonso, 2003; *Cuatrecasas 10407** (COL). ***S. cubensis*** Britton & P. Wilson: Epling, 1939; S. Vogel, pers. comm.; *Howard 6170* (P); *Shafer 3766** (NY). ***S. curta*** Epling: Epling, 1939; Epling & Toledo, 1943; *Dusén 1283** (NY). ***S. curticalyx*** Epling: Epling, 1940a; *Penland & Summers 1191** (GH). ***S. curtiflora*** Epling: Epling, 1939; *Skutch 1972** (NY, US); *P. Wester 294* (MEXU, MJG, wild); *Williams et al. 23188* (TEX-LL). ***S. curviflora*** Benth.: Epling, 1939; *Graham 97** (K). ***S. cuspidata*** Ruiz & Pav.: Epling, 1939; Wood, 2007; *P. Wester 9*, *11*, *13* (LPB, MJG, wild). ***S. cyanantha*** Epling: Epling, 1940a; *Hinton 15350** (GH, NY, UC-JEPS, US); *Mexia 8729** (S). ***S. cyanicalyx*** Epling: Epling, 1941; *Schmidt-Lebuhn 578* (K, MJG, cult.); *Stork et al. 10618** (F). ***S. cyanocephala*** Epling: Epling, 1939; Wood & Harley, 1989; Fernández Alonso, 2003, 2006; *Wood 5000* (MEXU), *5409*, *5122* (K); *Fernández Alonso et al. 14605* (MEXU); *Fernández Alonso & Castillo 18917** (COL). ***S. cyanotropha*** Epling: Epling, 1939. ***S. cylindriflora*** Epling: Epling, 1939; *Pearce 565** (K).

S. darcyi J. Compton: Compton, 1994; *P. Wester 479*, *566* (MJG, cult.). ***S. dasycalyx*** Fernald: Epling, 1939. ***S. decumbens*** Alain: Liogier, 1973, 1994; *Liogier 17932** (NY). ***S. decurrens*** Epling: Epling, 1939; Epling & Toledo, 1943. ***S. densiflora*** Benth.: Epling, 1939; *Ekman 13924* (K). ***S. diamantina*** E. P. Santos & Harley: dos Santos & Harley, 2004. ***S. dichlamys*** Epling: Epling, 1939, 1940a; Epling & Játiva, 1966; Martínez & Matuda, 1984; *Hinton 914** (K, NY), *13956** (NY, TEX-LL, UC-JEPS, US). ***S. discolor*** Kunth: Epling, 1939; *Weberbauer 6069* (F); *P. Wester 574* (MJG, cult.). ***S. disjuncta*** Fernald: Epling, 1939; Standley & Williams, 1973; dos Santos, 1991; *Ghiesbreght 76** (NY), *753* (MO); *Nelson 3166* (US); *P. Wester 254* (MEXU, MJG, wild, cult.), *296*, *304* (BIGU, MEXU, MJG, wild). ***S. divinorum*** Epling & Játiva: Epling & Játiva, 1962; Reisfield, 1993; *Reisfield 1242* (K); *P. Wester 575* (MJG, cult.). ***S. dombeyi*** Epling: Mulsant & Verreaux, 1876; Epling, 1939; Macbride, 1960; Wood, 2007; *S. King 278* (F); *Mandon 712* (K); *Pearce 851* (K); *P. Wester* [*576–577*] (MJG, cult.). ***S. dorisiana*** Standl.: Standley, 1950; *P. Wester 578* (MJG, cult.); *Williams & Molina 13667** (US). ***S. dorrii*** (Kellogg) Abrams: Kellogg, 1863; Epling, 1938; Visco & Capon, 1970; Strachan, 1982; Neisess, 1983; Reisfield, 1987; *P. Wester 392*, *512*, *522*, *523* (MJG, wild), *600* (MJG, cult.). ***S. drymocharis*** Epling: Epling, 1939. ***S. dryophila*** Epling: Epling, 1939; *Hinton 5406** (NY). ***S. dugesiana*** Epling: Epling, 1939; *Dugès 226** (GH). ***S. durantiflora*** Epling: Epling, 1939; *Mexia 8944* (B). ***S. durifolia*** Epling: Epling, 1939; dos Santos, 1996. ***S. duripes*** Epling & Mathias: Epling & Mathias, 1957; *Matuda 5810**, *6010* (TEX-LL).

S. ecuadorensis Briq.: Epling, 1939; *Spruce 5543** (C, GH, GOET). ***S. eizi-matudae*** Ramamoorthy: Epling, 1939; Ramamoorthy, 1987; *Matuda 138** (UC-JEPS, US). ***S. elegans*** Vahl: Epling, 1939; Wagner, 1946; Dieringer et al., 1991; Van Devender et al., 2004; Lara, 2006; *Galeotti 685** (P); *P. Wester 156*, *193*, *214* (MJG, wild), *165* (MEXU, MJG, wild), *579* (MJG, cult.). ***S. emaciata*** Epling: Epling, 1939. ***S. engelmannii*** A. Gray: Whitehouse, 1949; *McVaugh 8297* (P); *P. Wester* [*360*] (MJG, cult.). ***S. eplingiana*** Alziar: Epling, 1949a; Alziar, 1988a; *Hinton 11260** (NY, TEX-LL). ***S. eremostachya*** Jeps.: Epling, 1938; Shreve & Wiggins, 1964; Neisess, 1983; *P. Wester 459* (MJG, wild, cult.), *460* (MJG, wild). ***S. eriocalyx*** Bertero ex Roem. & Schult.: Epling, 1939. ***S. ernesti-vargasii*** C. Nelson: Nelson, 1984; *Nelson 3678** (MO). ***S. erythrostephana*** Epling: Epling, 1951; Epling & Mathias, 1957; *Tucker 989* (K). ***S. erythrostoma*** Epling: Epling, 1939; Wood & Harley, 1989; Fernández Alonso, 1995c; *Fernández*

*Alonso 11913** (COL); *Killip 16772** (NY). ***S. espiritosantensis*** Brade & Barb. Per.: Brade & Barbosa, 1946; dos Santos, 1991; *Brade et al. 18369** (K). ***S. exilis*** Epling: Epling, 1940a; *Mexia 9097** (B, NY, TEX-LL). ***S. expansa*** Epling: Epling, 1951. ***S. exserta*** Griseb.: Epling, 1939, 1941; Wester & Claßen-Bockhoff, 2007; Wood, 2007; *Krapovickas 19167* (P); *Lorentz & Hieronymus 985** (UC-JEPS: slide with flower and copy of GOET); *P. Wester 22*, [*24*], *28* (MJG, wild), *27* (MJG, wild, cult.), *23* (LPB, MJG, wild, cult.).

S. falcata J. R. I. Wood & Harley: Wood & Harley, 1989; *Wood 4944* (K), *Wood 4962** (COL, K). ***S. fallax*** Fernald: Epling, 1939, 1941; *Palmer 1964** (C, NY, P). ***S. farinacea*** Benth.: Epling, 1939; *P. Wester 349* (MJG, wild). ***S. fernaldii*** Standl.: Epling, 1939. ***S. festiva*** Epling: Epling, 1939. ***S. filifolia*** Ramamoorthy: Ramamoorthy, 1983a. ***S. filipes*** Benth.: Epling, 1939; *Hartweg 375** (NY, P); *Hinton 9762** (TEX-LL). ***S. firma*** Fernald: Epling, 1939; *Palmer 61** (NY); *Pringle 8757* (P). ***S. flaccida*** Fernald: Epling, 1939; *Nelson 3374* (US); *von Türckheim 780** (GH, P, US). ***S. flaccidifolia*** Fernald: Epling, 1939, 1941; Reisfield, 1987; *Pringle 10298** (C, L, MO, NY, P, TEX-LL, US). ***S. flocculosa*** Benth.: Epling, 1939; *Hartweg 1347** (F). ***S. florida*** Benth.: Epling, 1939, 1941; *Schmidt-Lebuhn 450* (K, MJG, cult.); *Wasshausen 949* (K). ***S. fluviatilis*** Fernald: Epling, 1939; Dieringer et al., 1991; *Pringle 6850** (P). ***S. formosa*** L'Hér.: Ruiz & Pavon, 1798; Mirbel, 1810; Epling, 1939; *Mathews 799* (K); *Sandeman 5/34* (K); *Stork & Horton 9387* (K); *Woytkowski 34003* (F). ***S. forreri*** Greene: Epling, 1939; *Pringle 10104* (P). ***S. foveolata*** Urb. & Ekman: Torke, 2000; *Ekman H7737a, H7799* (K); *Torke 84* (FLAS). ***S. fracta*** L. O. Williams: Standley & Williams, 1973. ***S. fruticetorum*** Benth.: Schmidt, 1858; Epling, 1939; Epling & Toledo, 1943; *Prinz Maximilian zu Neuwied s.n.* (K). ***S. fruticulosa*** Benth.: Epling, 1939; *Andrieux 151** (P). ***S. fulgens*** Cav.: Epling, 1939; Wagner, 1946; Ramamoorthy, 1984a, 2001; Reisfield, 1987; dos Santos, 1991; Wester & Claßen-Bockhoff, 2007; *M. Crone 15* (MJG); *P. Wester 159* (MEXU, MJG, wild, cult.), [*181*] (MJG, wild). ***S. funckii*** Briq.: Epling, 1939; Wood & Harley, 1989; *Funck 280** (G). ***S. funerea*** M. E. Jones: Epling, 1938; Neisess, 1983; *P. Wester 490* (MJG, wild). ***S. fusca*** Epling: Epling, 1939; *Langlassé 216** (P). ***S. fuscomanicata*** Fern. Alonso: Fernández Alonso, 2003; *Sarria 475** (COL).

S. gachantivana Fern. Alonso: Fernández Alonso, 1995a; *Fernández Alonso 8217* (COL); *Wood 5153* (COL). ***S. galloana*** B. L. Turner: Turner, 2009b; *Martínez & Barrie 5678** (TEX-LL). ***S. gesneriiflora*** Lindl. & Paxton: Johow, 1901; Epling, 1939; dos Santos, 1991; Ramamoorthy, 2001; Schondube et al., 2004; *P. Wester 164, 194* (MEXU, MJG, wild), *213* (MJG, wild), *591* (MJG, cult.). ***S. glabra*** M. Martens & Galeotti: Epling, 1939. ***S. glechomifolia*** Kunth: Epling, 1939. ***S. goldmanii*** Fernald: Epling, 1939. ***S. gracilipes*** Epling: Epling, 1951; Wood & Harley, 1989. ***S. graciliramulosa*** Epling & Játiva: Epling & Játiva, 1966; Wood, 2007; *P. Wester 14* (LPB, MJG, wild, cult.). ***S. grandis*** Epling: Epling, 1944; Standley & Williams, 1973; *Steyermark 43047** (UC-JEPS). ***S. gravida*** Epling: Epling, 1940a, 1941; Wester & Claßen-Bockhoff, 2007; *Hinton 12355** (MO, NY, TEX-LL); *Santana & Benz 6602* (ZEA); *P. Wester 196* (MJG, wild, cult.). ***S. greatae*** Brandegee: Epling, 1938; Shreve & Wiggins, 1964; Neisess, 1983; Ross, 1991; *P. Wester 499* (MJG, UCR, wild), *481*, *482* (MJG, cult.). ***S. greggii*** A. Gray: Epling, 1939; Wester & Claßen-Bockhoff, 2007; *P. Wester 527* cultivar *alba* (MJG, cult.). ***S. grewiifolia*** S. Moore: Epling & Toledo, 1943; Wester & Claßen-Bockhoff, 2007; Wood, 2007; *P. Wester 15* (K, LPB, MJG, wild, cult.). ***S. grisea*** Epling & Mathias: Epling & Mathias, 1957; *Ferreyra 7628** (F). ***S. griseifolia*** Epling: Epling, 1939. ***S. guadalajarensis*** Briq.: Epling, 1939; *Pringle 4624** (NY, TEX-LL); ***S. guaranitica*** A. St.-Hil. ex Benth.: Epling, 1939; Suarez, 1965; Wester & Claßen-Bockhoff, 2007; *P. Wester 418*, *559* (MJG, cult.). ***S. gypsophila*** B. L. Turner: Turner, 2008c, 2008d; *Reveal & Atwood 3421** (TEX-LL).

S. haenkei Benth.: Epling, 1939; Wester & Claßen-Bockhoff, 2006a; Wood, 2007; *P. Wester 55*, *56*, *58*, *61*, *67*, *74*, *80–82*, *88* (MJG, wild, div. cult.), *65* (K, LPB, MJG, wild). ***S. haitiensis*** Urb.: Epling, 1939; Liogier, 1994. ***S. hamulus*** Epling: Epling, 1939; *Hinton 9884** (GH, NY, TEX-LL). ***S. hapalophylla*** Epling: Epling, 1939; *Wasshausen & Salas 1188* (K); *Weberbauer 7858** (F, UC-JEPS). ***S. harleyana*** E. P. Santos: dos Santos, 2004. ***S. hatschbachii*** E. P. Santos: dos Santos, 1994. ***S. heerii*** Regel: Trelease, 1882; Epling, 1939; photo C. Froissart. ***S. helianthemifolia*** Benth.: Epling, 1939; Dieringer et al., 1991; *Rzedowski 47803* (F). ***S. henryi*** A. Gray: Walker & Elisens, 2001; *R. Duncan s.n.* (UCR); *P. Wester 374* (MJG, cult.). ***S. herbacea*** Benth.: Epling, 1939. ***S. hermesiana*** Fern. Alonso: Fernández Alonso, 2002; *Hermes Cuadros 2299** (COL). ***S. herrerae*** Epling: Epling, 1939; *Herrera 3207** (F, UC-JEPS). ***S. heterofolia*** Epling & Mathias: Epling & Mathias, 1957; *Clark 7087** (NY). ***S. heterotricha*** Fernald: Epling, 1939; *Palmer 53** (NY). ***S. hidalgensis*** Miranda: Miranda, 1950; *Miranda 9451* (MEXU); *Medrano et al. 10071* (MEXU); *Rafael H. 6471* (MEXU). ***S. hilarii*** Benth.: Epling, 1939; Epling & Toledo, 1943; *W. Hoehne 4017* (K). ***S. hintonii*** Epling: Epling, 1939; *Hinton 10150** (GH, NY, TEX-LL, US). ***S. hirsuta*** Jacq.: Epling, 1939. ***S. hirta*** Kunth: Epling, 1939; *Hart 1363* (K); *Lewis et al. 2625* (K); *Penland 1200* (UC-JEPS); *Steyermark 53708* (F). ***S. hirtella*** Vahl: Epling, 1939; *Asplund 18001* (K); *Harling et al. 6862* (K); *Schmidt-Lebuhn 395* (K, MJG, cult.). ***S. hispanica*** L.: Epling, 1939; Fernández Alonso, 2003; *Pringle 8837 ½* (TEX-LL); *Williams 41161* (F). ***S. holwayi*** S. F. Blake: Epling, 1939, 1941; Standley & Williams, 1973; Ramamoorthy, 1984a; *Holway 579** (US); *P. Wester 287* (MEXU, MJG, wild), *291* (MJG, wild). ***S. hotteana*** Urb. & Ekman: Epling, 1939; Liogier, 1994; *Ekman H-2415** (NY). ***S. humboldtiana*** F. Dietr.: Epling, 1939.

S. igualensis Fernald: Epling, 1939; *Pringle 8418** (NY, S, TEX-LL). ***S. incumbens*** Urb. & Ekman: Epling, 1939; Liogier, 1973. ***S. incurvata*** Ruiz & Pav.: Ruiz & Pavon, 1798; Epling, 1939. ***S. indigocephala*** Ramamoorthy: Epling, 1940a; Ramamoorthy, 1983b; *Hinton 12792** (NY, TEX-LL). ***S. infuscata*** Epling: Epling, 1939. ***S. innoxia*** Epling & Mathias: Epling & Mathias, 1957. ***S. inornata*** Epling: Epling, 1939; *Purpus 5678** (NY). ***S. integrifolia*** Ruiz & Pav.: Epling, 1939; *Dombey 273** (P, US); *López & Sagástegui 3552* (UC-JEPS); *Lourteig 3262* (K); *Sandeman 5317* (K). ***S. intonsa*** Epling: Epling, 1939; Fernández Alonso, 2003; *Killip 16971* (GH, US). ***S. involucrata*** Cav.: Kunth, 1817; Epling, 1939; Epling & Mathias, 1957; Ramamoorthy, 1984a; *P. Wester* [*580*], *581* (MJG, cult.). ***S. iodantha*** Fernald: Epling, 1939; Dieringer et al., 1991; Lara & Ornelas, 2001; Schondube et al., 2004; Lara, 2006; *Pringle 8039** (NY, US); *P. Wester 212* (MJG, wild), *582* (MJG, cult.). ***S. iodophylla*** Epling: Epling, 1939; *Botteri 793** (K). ***S. ionocalyx*** Epling: Epling, 1939; *Matuda 134** (MO), *Matuda 1903* (K). ***S. itaguassuensis*** Brade & Barb. Per.: Brade & Barbosa, 1946; *Brade 18476** (NY). ***S. iuliana*** Epling: Epling, 1947; dos Santos, 1991; *Steyermark 56450** (UC-JEPS).

S. jacalana B. L. Turner ('*S. tarayensis* K. M. Peterson'): Peterson, 1978; Turner, 2008c, 2008d; *Mayfield et al. 820** (TEX-LL). ***S. jacobi*** Epling: Epling, 1940a; *Hinton 14110** (NY, TEX-LL). ***S. jaimehintoniana*** Ramamoorthy ex B. L. Turner: Turner, 1995b; *Burford L. Westlund 5.20.88.24** (TEX-LL). ***S. jamaicensis*** Fawc.: Epling, 1939; *Harris 7327** (NY). ***S. jaramilloi*** Fern. Alonso: Fernández Alonso, 2003. ***S. jorgehintoniana*** Ramamoorthy ex B. L. Turner: Turner, 1995a; *Hinton 21348** (K, TEX-LL).

S. karwinskii Benth.: Epling, 1939; Standley & Williams, 1973; Ramamoorthy, 1984a; Pool, 2001; *P. Wester 236, 307* (MEXU, MJG, wild), *571* (MJG, cult.). ***S. keerlii*** Benth.: Epling, 1939; Dieringer et al., 1991; Ramamoorthy, 2001. ***S. kellermanii*** Donn. Sm.: Epling, 1939, 1951; Epling & Mathias, 1957; Standley & Williams, 1973; Molina, 1975; Pool, 2001; *Kellerman 5628** (TEX-LL), *Maxon & Hay 3569** (US); *Williams & Molina 12232** (MO).

S. lachnaioclada Briq.: Torke, 2000; *Eggers 2594** (B, L); *Ekman H-5086** (NY). ***S. lachnostachys*** Benth.: Epling, 1939; Epling & Toledo, 1943. ***S. lachnostoma*** Epling: Epling, 1939. ***S. laevis*** Benth.: Epling, 1939; *Pringle 4155** (NY); *Purpus 5679** (NY). ***S. lamiifolia*** Jacq.: Epling, 1939; *Prior s.n.** (K). ***S. langlassei*** Fernald: Epling, 1939; *Langlassé 216** (P). ***S. languidula*** Epling: Epling, 1939; *Hinton 10351** (NY, TEX-LL). ***S. lanicalyx*** Epling: Epling, 1939. ***S. lanicaulis*** Epling & Játiva: Epling & Játiva, 1963; *López & Sagástegui 2729** (HUT, UC-JEPS); *Sagástegui et al. 8113* (K); *Sánchez Vega 7032* (F). ***S. lasiantha*** Benth.: Epling, 1939; Dieringer et al., 1991; *Pittier 746** (US); *Rose 2862** (US); *Sousa 1698* (MEXU); *P. Wester 248* (MEXU, MJG, wild), *258* (MJG, wild). ***S. lasiocephala*** Hook. & Arn.: Epling, 1939; *Palmer 295** (NY); *Smith 1371** (NY). ***S. lavanduloides*** Kunth: Epling, 1939; Dieringer et al., 1991; Schondube et al., 2004; *P. Wester 282* (MJG, wild). ***S. lavendula*** Alain: Liogier, 1988; Torke, 2000; *A. H. Liogier 12911** (NY, US). ***S. laxispicata*** Epling: Epling, 1939. ***S. leninae*** Epling: Epling, 1941; *Hinton 14897** (ARIZ, GH, NY, TEX-LL, US). ***S. lenta*** Fernald: Epling, 1939. ***S. leptostachys*** Benth.: Epling, 1939. ***S. leucantha*** Cav.: Epling, 1939; Wood & Harley, 1989; Ramamoorthy, 2001; Wester & Claßen-Bockhoff, 2007; *Pringle 8402* (US); *P. Wester 466*, [*583*] (MJG, cult.). ***S. leucocephala*** Kunth: Epling, 1939; *Asplund 6837* (K), *20501* (TEX-LL); *Camp E-3122* (K); *Lewis & Klitgaard 2298* (K); *Schmidt-Lebuhn 399* (K, MJG, cult.). ***S. leucochlamys*** Epling: Epling, 1940a. ***S. leucophylla*** Greene: Epling, 1938; Neisess, 1983; *P. Wester* [*393*] (MJG, wild), [*397*, *399*] (MJG, cult.). ***S. libanensis*** Rusby: Epling, 1939; Ahlenslager, 1984; Wood & Harley, 1989; *H. H. Smith 1380** (GH, NY, TEX-LL, US); *Viereck s.n.* (K). ***S. lineata*** Benth.: Epling, 1939; *M. Crone 12* (MJG, cult.); *Purpus 2579** (NY, UC-JEPS). ***S. littae*** Vis.: Epling, 1939; *P. Wester 281* (MEXU, MJG, wild). ***S. lobbii*** Epling: Epling, 1939; Luteyn, 1999; Fernández Alonso, 2006; *Lobb 293** (K, W); *Schmidt-Lebuhn 475* (K, MJG). ***S. longibracteolata*** E. P. Santos: dos Santos, 1994. ***S. longispicata*** M. Martens & Galeotti: Epling, 1939; Schondube et al., 2004; *Pringle 1798** (NA, NY), *8504** (C, L, S). ***S. longistyla*** Benth.: Epling, 1939; Dieringer et al., 1991; *P. Wester 268* (MEXU, MJG, wild), *570* (MJG, cult.). ***S. lophanthoides*** Fernald: Epling, 1939. ***S. loxensis*** Benth.: Epling, 1939. ***S. lozanii*** Fernald: Epling, 1939; *Pringle 8928** (C, NY). ***S. lycioides*** A. Gray: Epling, 1939; *Pringle 52** (GH), *790* (NY). ***S. lyrata*** L.: Fernald, 1950; Gleason, 1963; *P. Wester* [*361*] (MJG, cult.).

S. macellaria Epling: Epling, 1939; *Schaffner 330/667** (C, GH, NY); *Parry & Palmer 748* (GH). ***S. macrocalyx*** Gardner: Epling, 1939; dos Santos, 1991. ***S. macrophylla*** Benth.: Epling, 1939; Wood, 2007; *Asplund 18115* (B); *Schmidt-Lebuhn 446* (K, MJG, cult.). ***S. macrostachya*** Kunth: Epling, 1939; Wood & Harley, 1989; Fernández Alonso, 2003; *André s.n.* (K); *Asplund 7788* (K); *Holm-Nielson & Quintana 24724* (AAU, K). ***S. madrensis*** Seem.: Epling, 1944; *Breedlove 35690* (MEXU); *S. Barry David 483* (FLAS); *Seemann 2079** (UC-JEPS); *Taylor & Knees 382* (K); *P. Wester* [*584*], *601* (MJG, cult.). ***S. malvifolia*** Epling & Játiva: Epling & Játiva, 1963; *R. Moran 3940** (SD). ***S. manantlanensis*** Ramamoorthy: Ramamoorthy & Lorence, 1987. ***S. manaurica*** Fern. Alonso: Fernández Alonso, 2002, 2003; *Rangel 11157-A** (COL). ***S. marci*** Epling: Epling, 1939; Shreve & Wiggins, 1964; Wiggins, 1980; *Carter et al. 2053* (K); *H. S. Gentry 4143* (K, MEXU); *Jones 27298** (UC-JEPS); *R. Moran 7449* (SD). ***S. mattogrossensis*** Pilg.: Epling, 1939; Epling & Toledo, 1943; dos Santos, 2004. ***S. mazatlanensis*** Fernald: Epling, 1939. ***S. medusa*** Epling & Játiva: Epling & Játiva, 1963; Sagástegui et al., 2003; Fernández Alonso, 2006; *López & Sagástegui 3535** (HUT, UC-JEPS); *Sagástegui et al. 16328* (HAO). ***S. melaleuca*** Epling: Epling, 1939; Wood & Harley, 1989; G. Pérez et al., 2006; *Killip & Smith 19735** (GH, NY); *Wood 3763** (COL), *4330*, *4332*, *4503* (K). ***S. melissiflora*** Benth.: Epling, 1939; Epling & Toledo, 1943; Epling & Játiva, 1963; dos Santos, 2004; *Dusén 7784** (GH); *Ferreira 28* (K); *Hatschbach 30578* (K); *Kummrow 672* (K); *S. Vogel 1965/604* (WU). ***S. melissodora*** Lag.: Epling, 1939. ***S. mellifera*** Greene: Epling, 1938; Grant & Grant, 1964; Neisess, 1983; Reisfield, 1987; *P. Wester 391* (MJG, wild). ***S. mendax*** Epling: Epling, 1939; Molina, 1975; Neisess, 1983; *Skutch 641* (US). ***S. mentiens*** Pohl: Pohl, 1827; Epling, 1939; Epling & Toledo, 1943; Epling & Mathias, 1957; Epling & Játiva, 1963; *Anonymous s.n.* (WU 38020); *Ball s.n.* (K). ***S. mexiae*** Epling: Epling, 1939; *Mexia 1801** (NY). ***S. mexicana*** L.: Epling, 1939; Wagner, 1946; Des Granges, 1979; Reisfield, 1987; Dieringer et al., 1991; Arizmendi et al., 1996; Lara & Ornelas, 2001; Arizmendi et al., 2007. ***S. mexicana*** var. ***minor*** Benth.: *M. Crone s.n.* (MJG); *P. Wester 183* (MEXU, MJG, wild), [*228*] (MJG, wild), *547* (MJG, cult.). ***S. mexicana*** var. ***major*** Benth.: *P. Wester 200*, *203*, *263* (MEXU, MJG, wild), *204* (MJG, wild), *548* (MJG, cult.). ***S. micrantha*** Vahl: Epling, 1939, 1940d; Liogier, 1994; Pool, 2001. ***S. microdictya*** Urb. & Ekman: Epling, 1939; Liogier, 1994. ***S. microphylla*** Kunth: Epling, 1939; Grant & Grant, 1968; Standley & Williams, 1973; Van Devender et al., 2004; Wester & Claßen-Bockhoff, 2007; *Hansen 7679* (F); *P. Wester 244* (MEXU, MJG, wild), *155* (MJG, wild), *415*, *526* (var. *wislizenii*, MJG, cult.). ***S. minarum*** Briq.: dos Santos, 1996. ***S. miniata*** Fernald: Epling, 1939; 1940a; Standley & Williams, 1973; *Ghiesbreght 760** (GH); *Schipp S-632** (GH); *P. Wester 585* (MJG, cult.). ***S. misella*** Kunth: Epling, 1939; Liogier, 1994. ***S. mocinoi*** Benth.: Epling, 1939; Dieringer et al., 1991; Pool, 2001; *Martínez 434* (F); *Pringle 8035** (C, L, NY). ***S. modica*** Epling: Epling, 1939; *Hinton 22892* (K). ***S. mohavensis*** Greene: Neisess, 1983; Fenster et al., 2004; *Sanders 369* (UCR); *Ward s.n.* (ASU); *P. Wester 469* (MJG, cult.), *491–494*, *506*, *510*, *516–517* (MJG, wild), *507*, *508* (MJG, UCR, wild), *599* (MJG, cult.); Pinacate-form: *Sanders & Neisess 5658* (UCR); *P. Wester 504* (MJG, UCR, cult.). ***S. monantha*** Brandegee ex Epling: Epling, 1939. ***S. monclovensis*** Fernald: Epling, 1939; *Palmer 1096** (GH, US). ***S. moniliformis*** Fernald: Epling, 1939; *Purpus 170** (NY). ***S. montecristina*** Urb. & Ekman: Epling, 1939; Liogier, 1994; *Ekman H-13150** (NY). ***S. mornicola*** Urb. & Ekman: Epling, 1939; Liogier, 1994; *Ekman H-4940** (US). ***S. mucidiflora*** Fernald: Epling, 1939; *Palmer 187** (C, NY). ***S. muelleri*** Epling: Epling, 1939; *Mueller 145** (TEX-

LL). ***S. munzii*** Epling: Epling, 1938; Shreve & Wiggins, 1964; Neisess, 1983; *Epling & Robinson s.n.** (TEX-LL); *P. Wester 436* (MJG, cult.). ***S. muscarioides*** Fernald: Epling, 1939.

S. nana Kunth: Epling, 1939. ***S. neovidensis*** Benth.: Epling, 1939; *Prinz Maximilian zu Wied s.n.** (GOET). ***S. nepetoides*** Kunth: Epling, 1939. ***S. nervata*** M. Martens & Galeotti: Epling, 1939; Wester & Claßen-Bockhoff, 2007; *Nelson 3635** (US); *P. Wester 292* (BIGU, MEXU, MJG, wild). ***S. nervosa*** Benth.: Epling, 1939; dos Santos, 1996. ***S. nigrescens*** Alain (nom. illeg.): Liogier, 1956; *A. H. Liogier 3706** (NY). ***S. nitida*** (M. Martens & Galeotti) Benth.: Epling, 1939. ***S. novoleontis*** B. L. Turner: Turner, 2009b; *Hernandez et al. 2681** (TEX-LL). ***S. nubigena*** J. R. I. Wood & Harley: Wood & Harley, 1989; *Wood 5251** (COL), *5269* (K). ***S. nubilorum*** Epling & Játiva: Epling & Játiva, 1968; *Steyermark 96943** (UC-JEPS).

S. oaxacana Fernald: Epling, 1939; *P. Wester 259* (MEXU, MJG, wild). ***S. oblongifolia*** M. Martens & Galeotti: Epling, 1939. ***S. obtorta*** Epling: Epling, 1939. ***S. obumbrata*** Epling: Epling, 1939; *Killip & Smith 25311** (F, US). ***S. occidentalis*** Sw.: Epling, 1939; Wiggins, 1971; Liogier, 1994. ***S. occidua*** Epling: Epling, 1939; *Liebmann 15697** (C). ***S. occultiflora*** Epling: Epling, 1939; *Jahn 670** (US). ***S. ochrantha*** Epling: Epling, 1939; Epling & Mathias, 1957; Epling & Játiva, 1963; *Lewis 3145* (K); *López 1043*, *3183* (HUT). ***S. ocimifolia*** Epling: Epling, 1939; *Eggers 15053** (LD, US). ***S. oligantha*** Dusén: Epling, 1939; Epling & Toledo, 1943; *Dusén 234* (K, S); *Freitas 451*, *471* (K); *S. Vogel 1965/681* (WU). ***S. ombrophila*** Dusén: Epling, 1939; Brade, 1943; Epling & Toledo, 1943; Epling & Mathias, 1957; *dos Santos 132* (K); *Harley 20346*, *20346a*, *20342* (K). ***S. opertiflora*** Epling: Epling, 1941; *Steyermark 31469* (US). ***S. ophiocephala*** J. R. I. Wood: Wood, 2007. ***S. oppositiflora*** Ruiz & Pav.: Ruiz & Pavón, 1798; Epling, 1939; Macbride, 1960; *Pennell 13534* (F); *Schmidt-Lebuhn 423*, *464* (K, MJG, cult.). ***S. orbignaei*** Benth.: Epling, 1939, 1947; Wester & Claßen-Bockhoff, 2007; Wood, 2007; *P. Wester 39–42*, *44*, *45*, *47*, *48*, *51* (MJG, wild, div. cult.), *50* (K, LPB, MJG, wild). ***S. oreopola*** Fernald: Epling, 1939; *Pringle 7643* (US); *P. Wester 185* (MJG, wild). ***S. oresbia*** Fernald: Epling, 1939; *Parry & Palmer 740** (GH, NY); *Schaffner 333/666** (C, GH, GOET, MEXU, NY). ***S. orthostachys*** Epling: Epling, 1939; Wood & Harley, 1989; Fernández Alonso, 1995a; *Killip & Smith 20746** (GH); *Wood 4175** (COL), *4510* (K). ***S. ovalifolia*** A. St.-Hil. ex Benth.: Epling, 1939; dos Santos, 1996; *Hassler 4294** (NY). ***S. oxyphora*** Briq.: Epling, 1939; Wood, 2007; *P. Wester 16* (LPB, MJG, wild, cult.).

S. pachyphylla Epling ex Munz: Epling, 1938; Neisess, 1983; *P. Wester 500*, *502*, *519*, *520*, *521* (MJG, wild), *402*, *471*, *488* (MJG, cult.). ***S. pachypoda*** Briq.: dos Santos, 1996. ***S. palealis*** Epling: Epling, 1940a; *Hinton 14040** (K, NY, UC-JEPS, US). ***S. palifolia*** Kunth: Epling, 1939. ***S. pallida*** Benth.: Epling, 1939. ***S. palmeri*** A. Gray: Epling, 1939; *Palmer 259** (NY). ***S. pamplonitana*** Fern. Alonso: Fernández Alonso, 2003. ***S. pannosa*** Fernald: Epling, 1939; Dieringer et al., 1991; *Pringle 8593** (NY). ***S. pansamalensis*** Donn. Sm.: Epling, 1939; *von Türckheim 933** (GH, K, NY, US). ***S. paposana*** Phil.: Epling, 1939; *King 294* (F); *Soukup 1282* (F). ***S. paraguariensis*** Briq.: Epling, 1939; dos Santos, 1996; *Hassler 9237** (NY). ***S. paramicola*** Fern. Alonso: Fernández Alonso, 1995b, 2003; *J. Aguirre 850** (COL). ***S. parciflora*** Urb.: Epling, 1939; Liogier, 1994. ***S. parryi*** A. Gray: Epling, 1939. ***S. paryskii*** Skean & Judd: Skean & Judd, 1988; Torke, 2000; *Skean 2096** (GOET). ***S. patens*** Cav.: Epling, 1939; *P. Wester 563*, [*593*] (MJG, cult.). ***S. pauciserrata*** Benth.: Epling, 1939; Epling & Mathias, 1957; Wood & Harley, 1989; *Hartweg 1327** (P); *Lehmann 5826* (K); *Schmidt-Lebuhn 369* (subsp. *calocalicina*, K, MJG, cult.); *P. Wester 555* (subsp. *calocalicina*, MJG, cult.). ***S. paulwalleri*** B. L. Turner: Turner, 2009b; *Shannon 94** (TEX-LL). ***S. paupercula*** Epling: Epling, 1939. ***S. pavonii*** Benth.: Epling, 1939, 1941; *Lobb 82* (K); *McLean s.n.* (K); *Saunders 689* (K); *Stork 10956* (F). ***S. penduliflora*** Epling: Epling, 1939; *Weberbauer 7910** (F). ***S. peninsularis*** Brandegee: Epling, 1939; Shreve & Wiggins, 1964; Wiggins, 1980; *Brandegee s.n.** (UC-JEPS); *R. Moran 18786* (SD); photo J. Rebman (SD). ***S. pennellii*** Epling: Epling, 1939; *Pennell 17538** (GH, UC-JEPS, US). ***S. pentstemonoides*** Kunth & C. D. Bouché: Kunth & Bouché, 1848; Bentham, 1876; Gray, 1886; Correll & Johnston, 1970; Walker et al., 2004; Walker & Sytsma, 2007; *Lindheimer 460** (NY); *P. Wester* [*586*] (MJG, cult.). ***S. perblanda*** Epling: Epling, 1939; *Hinton 9946** (NY, TEX-LL). ***S. peregrina*** Epling: Epling, 1951; *Espinosa 1591** (UC-JEPS). ***S. pericona*** B. L. Turner: Turner, 2009a; *García et al. 2342** (TEX-LL). ***S. perlonga*** Fernald: Epling, 1939, 1947; *Breedlove 61837* (MEXU); *Nelson 2186** (GH, UC-JEPS, US); *P. Wester 273* (MJG, wild), *645* (MJG, cult.). ***S. perlucida*** Epling: Epling, 1939; *Killip 22350** (F). ***S. perplicata*** Epling: Epling, 1939; *Rose 13876** (NY). ***S. persicifolia*** A. St.-Hil.: Epling, 1939; dos Santos, 1991. ***S. personata*** Epling: Epling, 1939; Wood, 2007; *P. Wester 17* (LPB, MJG, wild, cult.). ***S. pexa*** Epling: Epling, 1939; Ramamoorthy & Elliott, 1998. ***S. phaenostemma*** Donn. Sm.: Epling, 1939; *Nelson 3736** (US). ***S. pichinchensis*** Benth.: Mansfeld, 1937; Epling, 1939; Fernández Alonso, 2006; Schmidt-Lebuhn, pers. comm.; *Jameson 797** (K, US); *Ollgard & Balslev 9815* (K); *Schmidt-Lebuhn 381* (K, MJG). ***S. pineticola*** Epling: Epling, 1941. ***S. pinguifolia*** (Fernald) Woot. & Standl.: Standley, 1924; Epling, 1939; Shreve & Wiggins, 1964; *Goldman 1501** (US); *Palmer 7* (NY). ***S. pinosiana*** Gladkova: Gladkova, 1996. ***S. platycheila*** A. Gray: Epling, 1939; Shreve & Wiggins, 1964; *Palmer 7* (US). ***S. platyphylla*** Briq.: Epling, 1939; *Pringle 2560** (NA, NY). ***S. plumosa*** Ruiz & Pav.: Ruiz & Pavon, 1798; Epling, 1939; *Dombey 270** (F, L, SEV). ***S. plurispicata*** Epling: Epling, 1939; *Hinton 13549* (F). ***S. podadena*** Briq.: Epling, 1939. ***S. polystachya*** Cav.: Epling, 1939; Wagner, 1946; Dieringer et al., 1991; *Pringle 3224** (NY), *13279** (MICH, TEX-LL, US). ***S. potus*** Epling: Epling, 1939. ***S. praestans*** Epling: Epling, 1940a; *Hinton 11095** (K, MO, UC-JEPS, US); *Hinton 14765** (UC-JEPS); *Martínez 5715* (MEXU, TEX-LL, XAL). ***S. praeterita*** Epling: Epling, 1939; *Ekman H-13963** (NY). ***S. prasiifolia*** Benth.: Epling, 1939. ***S. primuliformis*** Epling: Epling, 1939; Liogier, 1994; *Ekman H-9230** (C, NY, TEX-LL). ***S. pringlei*** B. L. Rob. & Greenm.: Epling, 1939; *Pringle 4564** (K, NY, P, TEX-LL, US); *Reveal 4029* (TEX-LL; and photos). ***S. procurrens*** Benth.: Epling, 1939; Epling & Toledo, 1943; Suarez, 1965. ***S. propinqua*** Benth.: Epling, 1939; dos Santos, 1996. ***S. prostrata*** Hook. f.: Epling, 1939; Wiggins, 1971. ***S. protracta*** Benth.: Epling, 1939; Dieringer et al., 1991; Espejo Serna & Ramamoorthy, 1993; *Mexia 1583** (NY); *Pringle 6013** (L, NY); *P. Wester 264* (MJG, wild). ***S. pruinosa*** Fernald: Epling, 1939. ***S. prunelloides*** Kunth: Epling, 1939; *Humboldt & Bonpland s.n.** (P); *Pringle 9159* (F). ***S. pseudoincisa*** Epling: Epling, 1940a. ***S. pseudomisella*** Moran & G. A. Levin: Levin & Moran, 1989; *Moran 29522** (NY). ***S. pseudopallida*** Epling: Epling, 1940a; *Muller 3226** (TEX-LL, US). ***S. pseudoprivoides*** Epling:

Epling, 1939. ***S. pseudorosmarinus*** Epling: Epling, 1941; *Stork 9968** (F, UC-JEPS). ***S. pseudoserotina*** Epling: Epling, 1939; Wiggins, 1971; Harley, 1999; *Darwin s.n.* (CGE). ***S. psilantha*** Epling: Epling, 1939; *Weberbauer 6590** (F, GH, UC-JEPS). ***S. psilostachya*** Epling: Epling, 1939; *Weberbauer 7141** (F, GH, UC-JEPS, US). ***S. pteroura*** Briq.: Epling, 1939. ***S. pubescens*** Benth.: Ahlenslager, 1984; *P. Wester 276* (MJG, wild). ***S. pulchella*** DC.: Epling, 1939; Ramamoorthy, 2001; *Pringle 8674** (MO, NY, P, TEX-LL, US). ***S. punctata*** Ruiz & Pav.: Epling, 1939. ***S. purpurea*** Cav.: Epling, 1939; Dieringer et al., 1991; Ramírez & Martínez, 1998; Ortiz-Pulido et al., 2002; *M. Crone s.n.* (MJG); *P. Wester 174, 190* (MEXU, MJG, wild), *205, 206, 216, 217, 242, 243*, [*229, 260, 286*] (MJG, wild). ***S. purpusii*** Brandegee: Epling, 1939. ***S. pusilla*** Fernald: Epling, 1939.

S. quercetorum Epling: Epling, 1939. ***S. quitensis*** Benth.: Lagerheim, 1899; Epling, 1939; *Fleming 36* (K); *Harling 6827* (F); *Jameson 711** (K, NY, P).

S. ramamoorthyana Espejo: Espejo Serna & Ramamoorthy, 1993; *Reveal 4106** (NY, TEX-LL). ***S. ramosa*** Brandegee: Epling, 1939; Turner, 2009a; *Purpus 2578** (UC-JEPS), *3288** (NY). ***S. raveniana*** Ramamoorthy: Ramamoorthy, 1984b; *Calzada 21603* (MEXU); *Manzanero 241* (OAX); *Ramamoorthy 4488* (K, MEXU); *Reyes 797* (MEXU); *Torres et al. 1926* (MEXU). ***S. raymondii*** J. R. I. Wood: Wood, 2007; *P. Wester 1* (MJG, wild). ***S. recurva*** Benth.: Epling, 1939; Reisfield, 1987. ***S. reflexa*** Hornem.: Epling, 1939. ***S. regla*** Cav.: Ahlenslager, 1984; *P. Wester 255* (MJG, wild), *356* (MJG, cult.). ***S. regnelliana*** Briq.: Briquet, 1904; Epling, 1939; Epling & Toledo, 1943; *Lindman 1261** (S). ***S. reitzii*** Epling: Epling, 1960. ***S. remissa*** Epling: Epling, 1939; *Mexia 1559** (NY). ***S. remota*** Benth.: Epling, 1939. ***S. reptans*** Jacq.: Peterson, 1978; Ramamoorthy, 2001. ***S. retinervia*** Briq.: Epling, 1939; Wood, 2007; *P. Wester 30* (LPB, MJG, wild). ***S. revoluta*** Ruiz & Pav.: Epling, 1939; *Macbride 3041* (F). ***S. rhinosina*** Griseb.: Epling, 1939; Wood, 2007. ***S. rhodostephana*** Epling: Epling, 1939, 1941; *Killip & Smith 23323** (UC-JEPS, NY, US); *Wasshausen & Encarnacíon 568* (K). ***S. rhombifolia*** Ruiz & Pav.: Epling, 1939; Wood, 2007; *Dombay s.n.** (P); *Lobb 293** (K). ***S. rhyacophila*** Epling: Epling, 1939; Dieringer et al., 1991. ***S. richardsonii*** B. L. Turner: Turner, 2008c, 2008d; *Richardson 1050** (TEX-LL). ***S. rivularis*** Gardner ex H. B. Fielding: Epling, 1939; Brade, 1943; dos Santos, 1991; *Brade 16371* (K); *Martinelli 12029* (K); *E. Pereira 247* (K). ***S. roemeriana*** Scheele: Walker & Elisens, 2001; *P. Wester 347, 350, 371*, [*348*] (MJG, wild), *564* (MJG, cult.). ***S. roscida*** Fernald: Epling, 1939; *Goldman 340** (NY). ***S. rosei*** Fernald: Fernald, 1900; Epling, 1939; *J. N. Rose 2844** (GH, US). ***S. rosmarinoides*** A. St.-Hil. ex Benth.: dos Santos, 1996; *Saint-Hilaire 2640** (P). ***S. rostellata*** Epling: Epling, 1939. ***S. rubescens*** Kunth: Epling, 1939; Wood & Harley, 1989; *Humboldt & Bonpland s.n.** (P); *P. Wester 442* (MJG, cult.); *Wood 4161** (COL). ***S. rubrifaux*** Epling: Epling, 1951; Jørgensen & Ulloa Ulloa, 1994; *Vargas 6955** (K, UC-JEPS). ***S. rubriflora*** Epling: Epling, 1951; Wood & Harley, 1989; Fernández Alonso, 2003; *Haught 5944** (COL, P, US); *Fernández Alonso & G. Perez 12600A* (K, MEXU); *Wood 3979, 4580, 4942* (K). ***S. rubropunctata*** B. L. Rob. & Fernald: Epling, 1939. ***S. rufula*** Kunth: Epling, 1939, 1941; Wood & Harley, 1989; Jørgensen & Ulloa Ulloa, 1994; Harley, 1999; *Cuatrecasas 8184** (F); *Hartweg 1326** (LD); *Rusby & Pennell 574** (NY); *Wood 5181** (COL), *4906, 5200, 5347* (K). ***S. rupicola*** Fernald: Epling, 1939. ***S. rusbyi*** Britton ex Rusby: Epling, 1939; *Bang 422* (NY); *Beck 9299, 18308* (K); *Gentry et al. 44226* (K); *Rusby 2414** (NY); *Solomon 9378* (K); *Solomon & Nee 12612* (K); *Solomon & Stein 11720* (K); *Solomon & Uehling 12228* (K); *Wasshausen & Salas 1206* (K); *Wood 13015* (K); *Wood & Mondaca 14545, 14574* (K); *Wood & Wasshausen 13755, 13928* (K); *P. Wester 31* (LPB, MJG, wild). ***S. rypara*** Briq.: Epling, 1939; Wood, 2007; *P. Wester 21, 33* (MJG, wild), *18, 32* (LPB, MJG, wild, cult.). ***S. rzedowskii*** Ramamoorthy: Ramamoorthy, 1984c.

S. saccifera Urb. & Ekman: Epling, 1939; Liogier, 1994. ***S. sacculus*** Epling: Epling, 1939. ***S. sagittata*** Ruiz & Pav.: Epling, 1939; Dorst, 1956; Wood & Harley, 1989; *Schmidt-Lebuhn 331* (K, MJG, cult.); *P. Wester 495* (MJG, cult.). ***S. salicifolia*** Pohl: Epling, 1939; Epling & Toledo, 1943; dos Santos et al., 2005; *Glaziou 18279* (P); *Irwin et al. 29119* (K). ***S. sanctae-luciae*** Seem.: Epling, 1939. ***S. sapinea*** Epling: Epling, 1941; Dieringer et al., 1991; *Hinton 14798** (NY, TEX-LL). ***S. sarmentosa*** Epling: Epling, 1939; *Pennell 13650** (F); *Vargas 297* (F). ***S. scabrata*** Britton & P. Wilson: Epling, 1939; *J. A. Shafer 4075** (NY; slides with flowers in UC-JEPS). ***S. scabrida*** Pohl: Epling, 1939; Epling & Toledo, 1943; dos Santos & Harley, 2004; *Arbo M. M. et al. 5248* (K); *Irwin et al. 25759* (K); *R. L. Mendonsa 305* (K). ***S. scandens*** Epling: Epling, 1939, 1944; *Weberbauer 7796** (US). ***S. scaposa*** Epling: Epling, 1939; *Hinton 5332** (NY, TEX-LL). ***S. sciaphila*** (J. R. I. Wood & Harley) Fern. Alonso: Wood & Harley, 1989; Fernando Alonso, 2003. ***S. scoparia*** Epling: Epling, 1960; *Reitz & Klein 17.831* (P). ***S. scutellarioides*** Kunth: Epling, 1939; Rasmussen, 2004; *Schmidt-Lebuhn 349, 380, 469* (K, MJG, cult.). ***S. scytinophylla*** Briq.: dos Santos, 1996; *Hassler 4532** (NY), *4725** (P). ***S. secunda*** Benth.: Epling, 1939, 1940a; dos Santos, 2004; *Forzza et al. 2841* (K); *Regnell III 932** (P); *Vauthier 408** (G, L). ***S. seemannii*** Fernald: Epling, 1939. ***S. selguapensis*** Ant. Molina: Molina, 1974. ***S. selleana*** Urb.: Epling, 1939; Liogier, 1994; Torke, 2000; *Buch 1145** (NY); *Fisher-Meerow 639* (FLAS); *Judd 4861* (FLAS). ***S. sellowiana*** Benth.: Epling, 1939; Epling & Toledo, 1943; *G. Gottsberger 36-9966, 21-9477* (K); *I. Gottsberger & G. Gottsberger 125-16471* (K); *Hatschbach & Pereira 11442, 11445* (K); *Hunt 6396* (K, P); *S. Vogel 1956/658* (WU). ***S. semiatrata*** Zucc.: Epling, 1939; Dieringer et al., 1991; *P. Wester 274, 275* (MJG, wild). ***S. serotina*** L.: Epling, 1939; *Parry & Palmer 751** (GH); *Pere Duss 265* (P). ***S. serpyllifolia*** Fernald: Epling, 1939; *Parry 751** (NY). ***S. serranoae*** J. R. I. Wood: Wood, 2007. ***S. sessei*** Benth.: Ahlenslager, 1984; Wester & Claßen-Bockhoff, 2007; *P. Wester* [*175*] (MJG, wild), *179, 219* (MEXU, MJG, wild). ***S. setosa*** Fernald: Epling, 1939; *Palmer 64** (K). ***S. setulosa*** Fernald: Epling, 1939; *Pringle 8403** (NY). ***S. shannonii*** Donn. Sm.: Epling, 1939. ***S. sharpii*** Epling & Mathias: Epling & Mathias, 1957; *Sharp 50132** (UC-JEPS). ***S. sigchosica*** Fern. Alonso: Fernández Alonso, 2006. ***S. silvarum*** Epling: Epling, 1939; *Killip 25612** (UC-JEPS); *Palmer 61* (K); *Schmidt-Lebuhn 545* (K, MJG). ***S. similis*** Brandegee: Epling, 1939. ***S. sinaloensis*** Fernald: Epling, 1939; Turner, 2009b. ***S. sochensis*** (J. R. I. Wood & Harley) Fern. Alonso: Fernández Alonso, 2003; see also Appendix 3; *Wood 5154** (COL). ***S. sonomensis*** Greene: Epling, 1938; Neisess, 1983; *P. Wester 431* (MJG, cult.). ***S. sophrona*** Briq.: Epling, 1939; Wood, 2007; *S. Vogel 1965/417* (WU); *P. Wester 34, 34a* (LPB, MJG, wild). ***S. sordida*** Benth.: Epling, 1939; Wood & Harley, 1989; Fernández Alonso, 2003; *Hartweg 1324** (LD), *Wood 4632* (K). ***S. sparsiflora*** Epling: Epling, 1944. ***S. spathacea*** Greene: Grant & Grant, 1968; Neisess, 1983; Wester & Claßen-Bockhoff, 2007; *P. Wester 444* (MJG, wild), [*400*], *544* (MJG, cult.). ***S. speciosa*** C.

Presl ex Benth.: Epling, 1939; *Ferreyra 14628* (K); *Macbride 1212* (F); *Sagástegui et al. 15681* (TEX-LL); *Sagástegui 9062* (K); *Sanchez Vega 2253* (CHAPA); *Sandeman 4638* (K). ***S. speirematoides*** C. Wright: Epling, 1939; *Wright 3657** (GH), *3757* (NY), *s.n.* (K). ***S. sphacelifolia*** Epling: Epling, 1939. ***S. sphacelioides*** Benth.: Epling, 1939; Wood & Harley, 1989; Fernández Alonso, 2003; *Smith 1381** (GH, NY, P, TEX-LL, US); *Wood 4975* (K), *5010** (COL). ***S. splendens*** Sellow ex Roem. & Schult.: Trelease, 1881; Epling, 1939; Epling & Toledo, 1943; dos Santos, 2004; Wester & Claßen-Bockhoff, 2007; *P. Wester 557* (MJG, cult.). ***S. sprucei*** Briq.: Epling, 1939; *Camp E-3974* (K); *Spruce 5990** (P). ***S. squalens*** Kunth: Kunth, 1817; Epling, 1939; Epling & Játiva, 1963; *Hutchinson & Wright 5432* (P); *P. Wester 498*, *592* (MJG, cult.). ***S. stachydifolia*** Benth.: Epling, 1939; Wood, 2007; *P. Wester 35* (LPB, MJG, wild, cult.). ***S. stachyoides*** Kunth: Epling, 1939; Dieringer et al., 1991. ***S. stolonifera*** Benth.: Bentham, 1839–1857; Epling, 1939; Lyon, 1976; Ramamoorthy, 1984a; *Hartweg 70** (L); *Pringle 4705* (UC-JEPS); *P. Wester 247* (MEXU, MJG, wild). ***S. striata*** Benth.: Epling, 1939; Macbride, 1960; *Schmidt-Lebuhn 575* (K, MJG, cult.), *s.n.* (MJG, cult.); *Stork & Horton 10667* (F). ***S. strobilanthoides*** C. Wright ex Griseb.: Epling, 1939; *Wright 3156** (GH, UC-JEPS). ***S. styphelus*** Epling: Epling, 1939; *Schmidt-Lebuhn 495* (K, MJG, cult.); *Smith 7356* (F). ***S. subaequalis*** Epling: Epling, 1939; Liogier, 1994; *Ekman H-8657a** (NY). ***S. subglabra*** (Urb.) Urb.: Epling, 1939; Liogier, 1994. ***S. subhastata*** Epling: Epling, 1939, 1940a; *Langlassé 570** (K). ***S. subincisa*** Benth.: Epling, 1939; *Hartweg 160** (K, L, NY). ***S. subobscura*** Epling: Epling, 1940a; *Hinton 12570** (NY, TEX-LL). ***S. subpatens*** Epling: Epling, 1939; *Hinton 4376** (GH, K, UC-JEPS, US). ***S. subrotunda*** A. St.-Hil. ex Benth.: Epling, 1939; *Balansa 1156** (P); *Saint-Hilaire B1024** (P); *S. Vogel 1965/551* (WU). ***S. subrubens*** Epling: Epling, 1939; Standley & Williams, 1973; *Heyde & Lux 3120** (US, UC-JEPS). ***S. subscandens*** Epling & Játiva: Epling & Játiva, 1968; *Hutchinson & Wright 3421** (UC-JEPS). ***S. sucrensis*** J. R. I. Wood: Wood, 2007; *P. Wester 142* (LPB, MJG, wild). ***S. summa*** A. Nelson: Walker & Elisens, 2001; *P. Wester 373* (MJG, cult.). ***S. synodonta*** Epling: Epling, 1940a; *Hinton 12576** (MO, NY, TEX-LL).

S. tafallae Benth.: Epling, 1939; Wood, 2007. ***S. tehuacana*** Fernald: Epling, 1939; *Pringle 8587** (TEX-LL). ***S. tenella*** Sw.: Epling, 1939; Liogier, 1994. ***S. tenorioi*** Ramamoorthy ex B. L. Turner: Turner, 2009a; *Tenorio & Frame 12291* (MEXU). ***S. tenuiflora*** Epling: Epling, 1939, 1960; *F. Müller 446* (K). ***S. tepicensis*** Fernald: Epling, 1939; *Palmer 1984** (NY). ***S. teresae*** Fernald: Epling, 1939. ***S. texana*** (Scheele) Torr.: Whitehouse, 1949; *P. Wester 351*, *362* (MJG, wild). ***S. textitlana*** B. L. Turner: Turner, 2009b. ***S. thomasiana*** Urb.: Epling, 1939. ***S. thormannii*** Urb.: Torke, 2000; *Torke 105* (FLAS); *v. Türckheim 3611** (K, L, P). ***S. thymoides*** Benth.: Epling, 1939; Dieringer et al., 1991. ***S. thyrsiflora*** Benth.: Epling, 1939; Dieringer et al., 1991; *Pringle 4097* (F). ***S. tiliifolia*** Vahl: Epling, 1939; Wood & Harley, 1987; Wood, 2007; *Pringle 8381** (TEX-LL); *P. Wester 36* (LPB, MJG, wild). ***S. tolimensis*** Kunth: Epling, 1939; Wood & Harley, 1989; *Purdie s.n.* (K); *Wood 5086* (K). ***S. tomentella*** Pohl: Pohl, 1827; Epling, 1939; Epling & Toledo, 1943; *Claussen 1538* (P); *Hatschbach et al. 36223* (K). ***S. tonalensis*** Brandegee: Epling, 1939; *Purpus 7006** (NY). ***S. tortuensis*** Urb.: Epling, 1939; Liogier, 1994. ***S. tortuosa*** Kunth: Epling, 1939; Gilli, 1983; Wood & Harley, 1989; see also Appendix 3; *E. W. D. & M. M. Holway 889** (US); *Humboldt & Bonpland s.n.** (P); *W. Jameson 685* (P); *Schmidt-Lebuhn 350*, *351* (K, MJG, cult.); *Gilli 284** (*S. corazonica* Gilli, W). ***S. townsendii*** Fernald: Epling, 1939; *Tenorio & Romero 1872* (K); *C. H. T. Townsend & Barber 426** (GH, MO, NY, P). ***S. trachyphylla*** Epling: Mansfeld, 1937; Epling, 1939; *Grubb et al. 224* (K); *Harling et al. s.n.* (K); *Pachano 202** (US). ***S. trichopes*** Epling: Epling, 1941; *Woodson & Schery 693** (GH, MO). ***S. trichostephana*** Epling: Epling, 1941; *Gentry 5846** (MO, UC-JEPS). ***S. tricuspidata*** M. Martens & Galeotti: Epling, 1939. ***S. trifilis*** Epling: Epling, 1941; *Stork & Horton 10105** (F). ***S. tubifera*** Cav.: Cavanilles, 1791; Epling, 1939, 1941; Ramamoorthy, 1984c; *P. Wester 231* (B, BIGU, JEPS, K, MEXU, MJG, TEX, wild). ***S. tubiflora*** Sm.: Ruiz & Pavón, 1798; Epling, 1939; Macbride, 1960; *Dombey s.n.** (P); photo Froissart. ***S. tubulosa*** Epling: Epling, 1939; *Pearce 261** (K); *Smith et al. 1779* (K). ***S. tuerckheimii*** Urb.: Torke, 2000; *von Türckheim 2896** (L, NY, US); *Ekman H-13625** (GH, K, NY, S, TEX-LL, US), *H-13947** (K, S). ***S. turneri*** Ramamoorthy: Turner, 1996b. ***S. tuxtlensis*** Ramamoorthy: Ramamoorthy, 1984d.

S. uliginosa Benth.: Epling, 1939; *P. Wester 588* (MJG, cult.). ***S. umbraticola*** Epling: Epling, 1939. ***S. umbratilis*** Fernald: Epling, 1939; *Langlassé 904** (GH, K, P). ***S. uncinata*** Urb.: Torke, 2000; *Ekman H13760** (K); *Howard & Howard 9155* (UC-JEPS). ***S. unguella*** Epling: Epling, 1940a; *Penland 1173** (COLO). ***S. unicostata*** Fernald: Epling, 1939; *Parry 760** (NY). ***S. univerticillata*** Ramamoorthy ex Klitg.: Klitgaard, 2007; *P. Wester 423* (MJG, cult.), *594* (MEXU, MJG, cult.). ***S. uribei*** J. R. I. Wood & Harley: Wood & Harley, 1989; *Wood 4939** (COL). ***S. urica*** Epling: Epling, 1939. ***S. urolepis*** Fernald: Epling, 1939. ***S. urticifolia*** L.: Epling, 1939; *Clayton 292** (BM). ***S. uruapana*** Fernald: Epling, 1939; *Pringle 13280** (TEX-LL).

S. vargasii Epling: Epling, 1947. ***S. vaseyi*** (Porter) Parish: Epling, 1938; Shreve & Wiggins, 1964; Neisess, 1983; *P. Wester 408*, *409*, *465* (MJG, wild). ***S. venulosa*** Epling: Epling, 1939; Wood & Harley, 1989; *Pennell 10616** (US); *Wood 5381*, *5384* (K). ***S. verapazana*** B. L. Turner: Turner, 1996a; *Contreras 11224** (TEX-LL). ***S. verecunda*** Epling: Epling, 1939. ***S. veronicifolia*** A. Gray ex S. Watson: Epling, 1939; *Palmer 28** (NY). ***S. vestita*** Benth.: Bentham, 1848; Epling, 1939; *Lobb s.n.** (K). ***S. villosa*** Fernald: Epling, 1939. ***S. viscida*** A. St.-Hil. ex Benth.: Epling, 1939; dos Santos, 1996; *Saint-Hilaire 34** (P). ***S. viscidifolia*** Epling: Epling, 1940a; *Hinton 10725**, *12369* (K). ***S. vitifolia*** Benth.: Epling, 1939; *Reveal et al. 4191* (K).

S. wagneriana Pol.: Epling, 1939, 1940b; Nowicke & Epling, 1969; Standley & Williams, 1973; Ramamoorthy, 1984a; Pool, 2001; *P. Wester 285* (BIGU, MEXU, MJG, wild), *443* (MJG, cult.); *White & White 321* (MO). ***S. weberbaueri*** Epling: Epling, 1939; *Weberbauer 6638** (GH). ***S. white-foordiae*** Klitg.: Klitgaard, 2007. ***S. whitehousei*** Alziar: Whitehouse, 1949; *Correll D. S. 38529* (TEX-LL); *McVaugh 7930* (P); *P. Wester 352* (MJG, TEX, wild), *353*, *367*, *524* (MJG, wild).

S. xalapensis Benth.: Epling, 1939; *v. Schlechtendal 93** (NY). ***S. xanthophylla*** Epling & Játiva: Epling & Játiva, 1963; *Hutchinson 6185* (P); *López & Sagástegui 2730** (HUT). ***S. xanthotricha*** Harley ex E. P. Santos: dos Santos, 2004. ***S. xeropapillosa*** Fern. Alonso: Fernández Alonso, 1995a, 2003; *Langenheim 3584** (COL).

S. yukoyukparum Fern. Alonso: Fernández Alonso, 2008.

S. zacualpanensis Briq.: Epling, 1939. ***S. zacuapanensis*** Brandegee: Epling, 1939; *Purpus 1932* (GH, US). ***S. zaragozana*** B. L. Turner: Turner, 2008c, 2008d.

Appendix 2. Pollination syndromes of New World *Salvia* species.

Ornithophilous (184 spp.)

S. acuminata Ruiz & Pav., *S. adenophora* Fernald, *S. alborosea* Epling & Játiva, *S. altimitrata* Epling, *S. altissima* Pohl, *S. apparicii* Brade & Barb. Per., *S. arbuscula* Fernald, *S. arduinervis* Urb. & Ekman, *S. articulata* Epling, *S. atrocaulis* Fernald, *S. atrocyanea* Epling, *S. ayavacensis* Kunth

S. bahorucona Urb. & Ekman, *S. balaustina* Pohl, *S. benthamiana* Gardner, *S. betulifolia* Epling, *S. blepharophylla* Brandegee ex Epling, *S. booleana* B. L. Turner, *S. buchananii* Hedge

S. cacaliifolia Benth., *S. camarifolia* Benth., *S. chapadensis* E. P. Santos & Harley, *S. cinnabarina* M. Martens & Galeotti, *S. clarkcowanii* B. L. Turner, *S. coccinea* Buc'hoz ex Etl., *S. cocuyana* Fern. Alonso, *S. confertiflora* Pohl, *S. cubensis* Britton & P. Wilson, *S. curtiflora* Epling, *S. curviflora* Benth., *S. cyanocephala* Epling, *S. cylindriflora* Epling

S. darcyi J. Compton, *S. diamantina* E. P. Santos & Harley, *S. disjuncta* Fernald, *S. divinorum* Epling & Játiva, *S. dombeyi* Epling, *S. dorisiana* Standl., *S. dugesiana* Epling

S. elegans Vahl, *S. ernesti-vargasii* C. Nelson, *S. erythrostephana* Epling, *S. espirito-santensis* Brade & Barb. Per., *S. exserta* Griseb.

S. falcata J. R. I. Wood & Harley, *S. florida* Benth., *S. formosa* L'Hér., *S. foveolata* Urb. & Ekman, *S. fruticetorum* Benth., *S. fulgens* Cav., *S. funckii* Briq.

S. gachantivana Fern. Alonso, *S. gesneriiflora* Lindl. & Paxton, *S. graciliramulosa* Epling & Játiva, *S. grandis* Epling, *S. gravida* Epling, *S. greggii* A. Gray, *S. grewiifolia* S. Moore, *S. guaranitica* A. St.-Hil. ex Benth.

S. haenkei Benth., *S. hapalophylla* Epling, *S. harleyana* E. P. Santos, *S. hatschbachii* E. P. Santos, *S. heerii* Regel, *S. henryi* A. Gray, *S. herrerae* Epling, *S. hidalgensis* Miranda, *S. hilarii* Benth., *S. hirta* Kunth, *S. hirtella* Vahl, *S. holwayi* S. F. Blake

S. integrifolia Ruiz & Pav., *S. involucrata* Cav., *S. iodantha* Fernald, *S. iodophylla* Epling, *S. itaguassuensis* Brade & Barb. Per., *S. iuliana* Epling

S. jorgehintoniana Ramamoorthy ex B. L. Turner

S. karwinskii Benth.

S. lachnaioclada Briq., *S. lachnostoma* Epling, *S. lanicaulis* Epling & Játiva, *S. lasiantha* Benth., *S. lavendula* Alain, *S. leucantha* Cav., *S. leucocephala* Kunth, *S. libanensis* Rusby, *S. lineata* Benth., *S. littae* Vis., *S. lobbii* Epling, *S. longibracteolata* E. P. Santos, *S. longistyla* Benth.

S. macrocalyx Gardner, *S. macrophylla* Benth., *S. madrensis* Seem., *S. marci* Epling, *S. mattogrossensis* Pilg., *S. medusa* Epling & Játiva, *S. melaleuca* Epling, *S. melissiflora* Benth., *S. mentiens* Pohl, *S. microphylla* Kunth, *S. miniata* Fernald

S. neovidensis Benth., *S. nervata* M. Martens & Galeotti, *S. nigrescens* Alain (nom. illeg.).

S. oaxacana Fernald, *S. ombrophila* Dusén, *S. oppositiflora* Ruiz & Pav., *S. orbignaei* Benth., *S. orthostachys* Epling, *S. oxyphora* Briq.

S. palealis Epling, *S. paramicola* Fern. Alonso, *S. paryskii* Skean & Judd, *S. patens* Cav., *S. pauciserrata* Benth., *S. pavonii* Benth., *S. peninsularis* Brandegee, *S. pentstemonoides* Kunth & C. D. Bouché, *S. persicifolia* A. St.-Hil., *S. phaenostemma* Donn. Sm., *S. pichinchensis* Benth., *S. plumosa* Ruiz & Pav., *S. pringlei* B. L. Rob. & Greenm., *S. psilantha* Epling, *S. pubescens* Benth., *S. pulchella* DC.

S. quitensis Benth.

S. raveniana Ramamoorthy, *S. regla* Cav., *S. regnelliana* Briq., *S. rhodostephana* Epling, *S. rivularis* Gardner ex H. B. Fielding, *S. roemeriana* Scheele, *S. rosei* Fernald, *S. rubescens* Kunth, *S. rubrifaux* Epling, *S. rubriflora* Epling, *S. rufula* Kunth, *S. rusbyi* Britton ex Rusby

S. sagittata Ruiz & Pav., *S. salicifolia* Pohl, *S. scabrata* Britton & P. Wilson, *S. scabrida* Pohl, *S. scandens* Epling, *S. sciaphila* (J. R. I. Wood & Harley) Fern. Alonso, *S. secunda* Benth., *S. sellowiana* Benth., *S. sessei* Benth., *S. sigchosica* Fern. Alonso, *S. spathacea* Greene, *S. speciosa* C. Presl ex Benth., *S. speirematoides* C. Wright, *S. splendens* Sellow ex Roem. & Schult., *S. sprucei* Briq., *S. squalens* Kunth, *S. stolonifera* Benth., *S. striata* Benth., *S. subhastata* Epling, *S. subrotunda* A. St.-Hil. ex Benth., *S. subrubens* Epling, *S. summa* A. Nelson

S. tenuiflora Epling, *S. thormannii* Urb., *S. tolimensis* Kunth, *S. tomentella* Pohl, *S. tortuosa* Kunth (including *S. corazonica* Gilli), *S. townsendii* Fernald, *S. trachyphylla* Epling, *S. tubifera* Cav., *S. tubiflora* Sm., *S. tubulosa* Epling, *S. tuerckheimii* Urb.

S. uncinata Urb., *S. unguella* Epling, *S. univerticillata* Ramamoorthy ex Klitg.

S. venulosa Epling, *S. verapazana* B. L. Turner, *S. vestita* Benth.

S. wagneriana Pol., *S. weberbaueri* Epling

S. xanthotricha Harley ex E. P. Santos, *S. xeropapillosa* Fern. Alonso

Melittophilous (351 spp.)

S. acerifolia B. L. Turner, *S. aequidistans* Fernald, *S. agnes* Epling, *S. alamosana* Rose, *S. alariformis* L. O. Williams, *S. alba* J. R. I. Wood, *S. albiflora* M. Martens & Galeotti, *S. albocaerulea* Linden, *S. aliciae* E. P. Santos, *S. alvajaca* Oerst., *S. amarissima* Ortega, *S. amissa* Epling, *S. amplifrons* Briq., *S. anastomosans* Ramamoorthy, *S. anguicoma* Epling, *S. angulata* Benth., *S. apiana* Jeps., *S. aratocensis* (J. R. I. Wood & Harley) Fern. Alonso, *S. areolata* Epling, *S. aridicola* Briq., *S. arizonica* A. Gray, *S. arthrocoma* Fernald, *S. assurgens* Kunth, *S. austromelissodora* Epling & Játiva, *S. axillaris* Moç. & Sessé ex Benth., *S. axilliflora* Epling, *S. azurea* Michx. ex Lam.

S. ballotiflora Benth., *S. betonica* Schult., *S. biserrata* M. Martens & Galeotti, *S. boegei* Ramamoorthy, *S. bogotensis* Benth., *S. borjensis* E. P. Santos, *S. brachyodonta* Briq., *S. brachyphylla* Urb., *S. brandegeei* Munz, *S. breviflora* Moç. & Sessé ex Benth., *S. brevipes* Benth.

S. caaguazuensis Briq., *S. cabonii* Urb., *S. calaminthifolia* Vahl, *S. calcicola* Harley, *S. californica* Brandegee, *S. calolophos* Epling, *S. campicola* Briq., *S. candicans* M. Martens & Galeotti, *S. capillosa* Epling, *S. cardenasii* J. R. I. Wood, *S. cardiophylla* Benth., *S. carduacea* Benth., *S. caudata* Epling, *S. caymanensis* Millsp. & Uline ex Millsp., *S. cedrosensis* Greene, *S. cerradicola* E. P. Santos, *S. chalarothyrsa* Fernald, *S. chamaedryoides* Cav., *S. chapalensis* Briq., *S. chazaroana* B. L. Turner, *S. chicamochae* J. R. I. Wood & Harley, *S. chionophylla* Fernald, *S. clarendonensis* Britton, *S. clinopodioides* Kunth, *S. coahuilensis* Fernald, *S. codazziana* Fern. Alonso, *S. cognata* Urb. & Ekman, *S. collinsii* Donn. Sm., *S. colonica* Standl. & L. O. Williams ex Klitg., *S. columbariae* Benth., *S. comayaguana* Standl., *S. compsostachys* Epling, *S. congestifolia* Epling, *S. connivens* Epling, *S. consimilis* Epling, *S. consobrina* Epling, *S. cordata* Benth., *S. corrugata* Vahl, *S. costaricensis* Oerst., *S. coulteri* Fernald, *S. crucis* Epling, *S. cruckshanksii* Benth., *S. cryptodonta* Fernald, *S. cuatrecasana* Epling, *S. curta* Epling, *S. curticalyx* Epling,

S. cuspidata Ruiz & Pav., *S. cyanantha* Epling, *S. cyanicalyx* Epling, *S. cyanotropha* Epling

S. dasycalyx Fernald, *S. decumbens* Alain, *S. decurrens* Epling, *S. densiflora* Benth., *S. dorrii* (Kellogg) Abrams, *S. drymocharis* Epling, *S. dryophila* Epling, *S. durantiflora* Epling, *S. durifolia* Epling, *S. duripes* Epling & Mathias

S. emaciata Epling, *S. engelmannii* A. Gray, *S. eplingiana* Alziar, *S. eriocalyx* Bertero ex Roem. & Schult., *S. exilis* Epling, *S. expansa* Epling

S. fallax Fernald, *S. farinacea* Benth., *S. fernaldii* Standl., *S. festiva* Epling, *S. filifolia* Ramamoorthy, *S. filipes* Benth., *S. firma* Fernald, *S. flaccida* Fernald, *S. flaccidifolia* Fernald, *S. flocculosa* Benth., *S. fluviatilis* Fernald, *S. forreri* Greene, *S. fracta* L. O. Williams, *S. fruticulosa* Benth., *S. fusca* Epling, *S. fuscomanicata* Fern. Alonso

S. galloana B. L. Turner, *S. glabra* M. Martens & Galeotti, *S. glechomifolia* Kunth, *S. goldmanii* Fernald, *S. gracilipes* Epling, *S. grisea* Epling & Mathias, *S. griseifolia* Epling, *S. guadalajarensis* Briq., *S. gypsophila* B. L. Turner

S. haitiensis Urb., *S. hamulus* Epling, *S. helianthemifolia* Benth., *S. herbacea* Benth., *S. hermesiana* Fern. Alonso, *S. heterofolia* Epling & Mathias, *S. heterotricha* Fernald, *S. hintonii* Epling, *S. hirsuta* Jacq., *S. hispanica* L., *S. hotteana* Urb. & Ekman, *S. humboldtiana* F. Dietr.

S. igualensis Fernald, *S. incumbens* Urb. & Ekman, *S. incurvata* Ruiz & Pav., *S. indigocephala* Ramamoorthy, *S. infuscata* Epling, *S. innoxia* Epling & Mathias, *S. inornata* Epling, *S. intonsa* Epling

S. jacalana B. L. Turner, *S. jacobi* Epling, *S. jaimehintoniana* Ramamoorthy ex B. L. Turner, *S. jamaicensis* Fawc., *S. jaramilloi* Fern. Alonso

S. keerlii Benth.

S. lachnostachys Benth., *S. laevis* Benth., *S. lamiifolia* Jacq., *S. langlassei* Fernald, *S. languidula* Epling, *S. lanicalyx* Epling, *S. lasiocephala* Hook. & Arn., *S. lavanduloides* Kunth, *S. laxispicata* Epling, *S. leninae* Epling, *S. lenta* Fernald, *S. leptostachys* Benth., *S. leucochlamys* Epling, *S. leucophylla* Greene, *S. longispicata* M. Martens & Galeotti, *S. lophanthoides* Fernald, *S. loxensis* Benth., *S. lozanii* Fernald, *S. lycioides* A. Gray, *S. lyrata* L.

S. malvifolia Epling & Játiva, *S. manantlanensis* Ramamoorthy, *S. manaurica* Fern. Alonso, *S. mazatlanensis* Fernald, *S. melissodora* Lag., *S. mellifera* Greene, *S. mexiae* Epling, *S. micrantha* Vahl, *S. minarum* Briq., *S. misella* Kunth, *S. mocinoi* Benth., *S. monantha* Brandegee ex Epling, *S. monclovensis* Fernald, *S. moniliformis* Fernald, *S. montecristina* Urb. & Ekman, *S. mornicola* Urb. & Ekman, *S. mucidiflora* Fernald, *S. munzii* Epling, *S. muscarioides* Fernald

S. nana Kunth, *S. nepetoides* Kunth, *S. nervosa* Benth., *S. nitida* (M. Martens & Galeotti) Benth., *S. novoleontis* B. L. Turner

S. oblongifolia M. Martens & Galeotti, *S. obtorta* Epling, *S. occidentalis* Sw., *S. occidua* Epling, *S. occultiflora* Epling, *S. ocimifolia* Epling, *S. oligantha* Dusén, *S. ophiocephala* J. R. I. Wood, *S. oreopola* Fernald, *S. ovalifolia* A. St.-Hil. ex Benth.

S. pachypoda Briq., *S. palifolia* Kunth, *S. pallida* Benth., *S. palmeri* A. Gray, *S. pamplonitana* Fern. Alonso, *S. pannosa* Fernald, *S. paposana* Phil., *S. paraguariensis* Briq., *S. parciflora* Urb., *S. parryi* A. Gray, *S. paulwalleri* B. L. Turner, *S. paupercula* Epling, *S. penduliflora* Epling, *S. pennellii* Epling, *S. perblanda* Epling, *S. peregrina* Epling, *S. pericona* B. L. Turner, *S. perlucida* Epling, *S. perplicata* Epling, *S. personata* Epling, *S. pineticola* Epling, *S. pinguifolia* (Fernald) Woot. & Standl., *S. pinosiana* Gladkova, *S. platycheila* A. Gray, *S. platyphylla* Briq., *S. plurispicata* Epling, *S. podadena* Briq., *S. polystachya* Cav., *S. potus* Epling, *S. praeterita* Epling, *S. prasiifolia* Benth., *S. primuliformis* Epling, *S. procurrens* Benth., *S. propinqua* Benth., *S. prostrata* Hook. f., *S. protracta* Benth., *S. pruinosa* Fernald, *S. prunelloides* Kunth, *S. pseudoincisa* Epling, *S. pseudomisella* Moran & G. A. Levin, *S. pseudopallida* Epling, *S. pseudoprivoides* Epling, *S. pseudoserotina* Epling, *S. pteroura* Briq., *S. purpusii* Brandegee, *S. pusilla* Fernald

S. quercetorum Epling

S. ramamoorthyana Espejo, *S. ramosa* Brandegee, *S. raymondii* J. R. I. Wood, *S. reflexa* Hornem., *S. reitzii* Epling, *S. remissa* Epling, *S. remota* Benth., *S. reptans* Jacq., *S. rhinosina* Griseb., *S. rhombifolia* Ruiz & Pav., *S. rhyacophila* Epling, *S. richardsonii* B. L. Turner, *S. roscida* Fernald, *S. rosmarinoides* A. St.-Hil. ex Benth., *S. rostellata* Epling, *S. rubropunctata* B. L. Rob. & Fernald, *S. rupicola* Fernald, *S. rypara* Briq., *S. rzedowskii* Ramamoorthy

S. saccifera Urb. & Ekman, *S. sacculus* Epling, *S. sanctae-luciae* Seem., *S. sapinea* Epling, *S. sarmentosa* Epling, *S. scaposa* Epling, *S. scoparia* Epling, *S. scytinophylla* Briq., *S. seemannii* Fernald, *S. selguapensis* Ant. Molina, *S. selleana* Urb., *S. serotina* L., *S. serpyllifolia* Fernald, *S. serranoae* J. R. I. Wood, *S. setosa* Fernald, *S. setulosa* Fernald, *S. shannonii* Donn. Sm., *S. similis* Brandegee, *S. sinaloensis* Fernald, *S. sochensis* (J. R. I. Wood & Harley) Fern. Alonso, *S. sonomensis* Greene, *S. sophrona* Briq., *S. sordida* Benth., *S. sparsiflora* Epling, *S. sphacelifolia* Epling, *S. sphacelioides* Benth., *S. stachydifolia* Benth., *S. stachyoides* Kunth, *S. styphelus* Epling, *S. subaequalis* Epling, *S. subglabra* (Urb.) Urb., *S. subincisa* Benth., *S. subobscura* Epling, *S. subpatens* Epling, *S. subscandens* Epling & Játiva, *S. sucrensis* J. R. I. Wood, *S. synodonta* Epling

S. tafallae Benth., *S. tehuacana* Fernald, *S. tenella* Sw., *S. tenorioi* Ramamoorthy ex B. L. Turner, *S. tepicensis* Fernald, *S. teresae* Fernald, *S. texana* (Scheele) Torr., *S. textitlana* B. L. Turner, *S. thomasiana* Urb., *S. thymoides* Benth., *S. thyrsiflora* Benth., *S. tiliifolia* Vahl, *S. tonalensis* Brandegee, *S. tortuensis* Urb., *S. trichopes* Epling, *S. tricuspidata* M. Martens & Galeotti, *S. trifilis* Epling, *S. turneri* Ramamoorthy, *S. tuxtlensis* Ramamoorthy

S. uliginosa Benth., *S. umbraticola* Epling, *S. unicostata* Fernald, *S. uribei* J. R. I. Wood & Harley, *S. urica* Epling, *S. urolepis* Fernald, *S. urticifolia* L., *S. uruapana* Fernald

S. vargasii Epling, *S. verecunda* Epling, *S. veronicifolia* A. Gray ex S. Watson, *S. villosa* Fernald, *S. viscida* A. St.-Hil. ex Benth., *S. vitifolia* Benth.

S. whitefoordiae Klitg.

S. xalapensis Benth., *S. xanthophylla* Epling & Játiva

S. zacualpanensis Briq., *S. zacuapanensis* Brandegee, *S. zaragozana* B. L. Turner

Psychophilous (1 sp.)

S. whitehousei Alziar

Intermediate (Ornithophilous, Melittophilous, Psychophilous)

ornithophilous, melittophilous, and/or intermediate (36 spp.)

S. angustiarum Epling, *S. arenaria* A. St.-Hil. ex Benth., *S. aspera* M. Martens & Galeotti, *S. atrocalyx* Epling, *S. atropaenulata* Epling, *S. bullulata* Benth., *S. camporum* Epling, *S. carbonoi* Fern. Alonso, *S. chiapensis* Fernald, *S. costata* Epling, *S. dichlamys* Epling, *S. ecuadorensis* Briq., *S.*

eizi-matudae Ramamoorthy, *S. erythrostoma* Epling, *S. ionocalyx* Epling, *S. kellermanii* Donn. Sm., *S. mendax* Epling, *S. modica* Epling, *S. muelleri* Epling, *S. nubigena* J. R. I. Wood & Harley, *S. nubilorum* Epling & Játiva, *S. obumbrata* Epling, *S. opertiflora* Epling, *S. oresbia* Fernald, *S. pansamalensis* Donn. Sm., *S. perlonga* Fernald, *S. pexa* Epling, *S. praestans* Epling, *S. pseudorosmarinus* Epling, *S. punctata* Ruiz & Pav., *S. purpurea* Cav., *S. revoluta* Ruiz & Pav., *S. sharpii* Epling & Mathias, *S. silvarum* Epling, *S. umbratilis* Fernald, *S. viscidifolia* Epling

ORNITHOPHILOUS TO ORNITHOPHILOUS, MELITTOPHILOUS, AND/OR INTERMEDIATE TO MELITTOPHILOUS (1 SP.)

S. carnea Kunth

ORNITHOPHILOUS TO ORNITHOPHILOUS, MELITTOPHILOUS, OR INTERMEDIATE (6 SPP.)

S. amethystina Sm., *S. concolor* Lamb. ex Benth., *S. mexicana* L., *S. ochrantha* Epling, *S. recurva* Benth., *S. semiatrata* Zucc.

MELITTOPHILOUS AND/OR INTERMEDIATE (7 SPP.)

S. ampelophylla Epling, *S. discolor* Kunth, *S. macellaria* Epling, *S. macrostachya* Kunth, *S. retinervia* Briq., *S. scutellarioides* Kunth, *S. yukoyukparum* Fern. Alonso

ORNITHOPHILOUS, PSYCHOPHILOUS, AND/OR INTERMEDIATE (4 SPP.)

S. chionopeplica Epling, *S. clevelandii* (A. Gray) Greene, *S. mohavensis* Greene, *S. pachyphylla* Epling ex Munz

MELITTOPHILOUS, PSYCHOPHILOUS, ORNITHOPHILOUS, AND/OR INTERMEDIATE (2 SPP.)

S. eremostachya Jeps., *S. vaseyi* (Porter) Parish

MELITTOPHILOUS, PSYCHOPHILOUS, AND/OR INTERMEDIATE (2 SPP.)

S. funerea M. E. Jones, *S. greatae* Brandegee

NOT ASSIGNABLE (LACKING DATA)

S. alata Epling, *S. arborescens* Urb. & Ekman, *S. brachyloba* Urb., *S. buchii* Urb., *S. microdictya* Urb. & Ekman, *S. psilostachya* Epling, *S. strobilanthoides* C. Wright ex Griseb., *S. trichostephana* Epling

APPENDIX 3. Taxonomic note.

Salvia tortuosa Kunth, Nov. Gen. Sp. [H.B.K.] 2: 292. 1818. TYPE: Colombia. *Humboldt & Bonpland s.n.* (holotype, P!).
Salvia corazonica Gilli, Feddes Repert. 94: 316. 1983, syn. nov. TYPE: Ecuador. El Corazon, 1630 m, 30 June 1975, *Gilli 284* (holotype, W!).

Salvia ampelophylla Epling, *S. aratocensis* (J. R. I. Wood & Harley) Fern. Alonso, and *S. sochensis* (J. R. I. Wood & Harley) Fern. Alonso might be also regarded as subspecies (*S. amethystina* J. E. Smith subsp. *ampelophylla* (Epling) J. R. I. Wood & Harley, *S. bogotensis* Benth. subsp. *aratocensis* J. R. I. Wood & Harley, and *S. bogotensis* Benth. subsp. *sochensis* J. R. I. Wood & Harley) (Wood & Harley, 1989; J. Wood, pers. comm.).

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—*Votis gratias agamus.*

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Cover illustration. *Emmotum yapacanum* R. A. Howard, drawn by Bruno Manara.

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A TAXONOMIC REVISION OF *GOUANIA* (RHAMNACEAE) IN MADAGASCAR AND THE OTHER ISLANDS OF THE WESTERN INDIAN OCEAN (THE COMORO AND MASCARENE ISLANDS, AND THE SEYCHELLES)[1]

Sven Buerki,[2] *Peter B. Phillipson,*[3,4] *and Martin W. Callmander*[3,5]

Abstract

A taxonomic revision of the genus *Gouania* Jacq. (Rhamnaceae) is presented for Madagascar and the other western Indian Ocean islands. Seventeen species are recognized, of which nine are described and published as new (all endemic to Madagascar): *G. ambrensis* Buerki, Phillipson & Callm., *G. callmanderi* Buerki, *G. cupreifolia* Buerki, Phillipson & Callm., *G. cupuliflora* Buerki, Phillipson & Callm., *G. gautieri* Buerki, Phillipson & Callm., *G. perrieri* Buerki, Phillipson & Callm., *G. phillipsonii* Buerki, *G. taolagnarensis* Buerki, Phillipson & Callm., and *G. zebrifolia* Buerki, Phillipson & Callm. Sixteen species occur in Madagascar, of which 13 are endemic and three are common to Madagascar and one or more of the smaller Indian Ocean islands. The latter include *G. laxiflora* Tul., a species which is also present on mainland Africa. One species, *G. mauritiana* Lam., is endemic to Réunion Island. We recognize two subspecies within *G. scandens* (Gaertn.) R. B. Drumm.: *G.*

[1] We would like to thank Professor Philippe Küpfer (Neuchâtel) and Nicolas Fumeaux (Genève) for helping S.B. during his Master's degree studies; Roger Lala Andriamiarisoa (Antananarivo) for his fine illustrations; Philippe Chassot (Neuchâtel) and Roy Gereau (St. Louis) for assistance with the Latin diagnoses; and the curators of the following herbaria for making material available for this study: G, K, MO, P, TAN, TEF, TUB, and WAG. Fieldwork was conducted under collaborative agreements between the Missouri Botanical Garden and the Parc Botanique et Zoologique de Tsimbazaza and the Direction de la Recherche Forestière et Piscicole, FOFIFA, Antananarivo, Madagascar. Financial support was provided to S.B. by the Fonds Wütrich in Neuchâtel, to P.B.P. and M.W.C. by the Andrew W. Mellon Foundation and the U.S. National Science Foundation (grant #0743355), and to M.W.C. by the National Institutes of Health, the U.S. National Science Foundation, and the U.S. Department of Agriculture under Cooperative Agreement U01 TW000313 with the International Cooperative Biodiversity Groups (ICBG). We also express our gratitude to our many friends and colleagues who have collected *Gouania* in Madagascar, and to Zachary Rogers, Laurent Gautier, an anonymous reviewer, and the Scientific Editor for providing valuable comments on the manuscript we originally submitted.

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scandens subsp. *scandens* and *G. scandens* subsp. *glandulosa* (Boivin ex Tul.) Buerki, Phillipson & Callm., the latter transferred from *G. glandulosa* Boivin ex Tul. Past confusion about the identity of this species is discussed. Five names are lectotypified: *G. aphrodes* Tul., *G. glandulosa* [= *G. scandens* subsp. *glandulosa*], *G. laxiflora*, *G. lineata* Tul., and *G. tiliifolia* Lam. Both lectotype and epitype are designated for *G. mauritiana*. Conservation assessments are provided for all species within their primary areas of occurrence.

Key words: Africa, Comoro Islands, *Gouania*, IUCN Red List, Madagascar, Mascarene Islands, Rhamnaceae, Seychelles.

The family Rhamnaceae is composed of 52 genera and 900 to 950 species (Medan & Schirarend, 2004). It comprises trees, shrubs, lianas, and a small number of herbs. Members of the family are easily recognized by their simple, alternate stipulate leaves that are often toothed and frequently possess strong parallel secondary veins and scalariform tertiary venation, and their small, (3 to)4- to 5(to 6)-merous flowers, which are haplostemonous with the stamens opposite the often clawed petals. The flowers possess a hypanthium with a nectary disc inside and have valvate calyx lobes that are ridged down the middle on the inner surface.

The pantropical genus *Gouania* Jacq. is comprised of 50 to 70 lianescent species (Mabberley, 2008). It is clearly separated from other genera of Rhamnaceae by the combination of the lianescent habit and the dry 3-winged schizocarp that separates into three 2-winged indehiscent mericarps (Medan & Schirarend, 2004). A recent phylogenetic analysis of Rhamnaceae based on *rbcL* and *trnL-F* sequences confirmed the monophyly of the tribe Gouanieae, and identified *Helinus* E. Mey. ex Endl. as the sister-group of *Gouania* (Richardson et al., 2000a, 2000b). The name *Gouania* commemorates Antoine Goüan (1733–1821), who was a professor at the University of Montpellier (France).

The taxonomy of the genus *Gouania* in the islands of the western Indian Ocean (Madagascar, the Comoro and Mascarene Islands, and the Seychelles) has not received much attention. Two species were described by Lamarck (1789), both from the Mascarene Islands, and later Tulasne (1857) described six species from Madagascar. The most recent treatment of *Gouania* for Madagascar and the Comoro Islands was published by Perrier de la Bâthie (1950). In this treatment, he recognized five species, three of which were subdivided into subspecies and varieties, and he placed three of Tulasne's Malagasy species in synonymy under *G. mauritiana* Lam. His treatment was based on less than 100 collections, all that were available at the time. Later, Guého (1979) recognized a new species on Rodrigues Island, bringing the total species count for the Mascarenes to three (Guého, 1997).

We present a taxonomic revision of the genus *Gouania* for the region, in which we recognize 17 species, nine of which are described as new. The classification proposed here relies essentially on the morphology of the plants, but it also presents a set of taxa with coherent distribution patterns, since biogeography and ecology play a vital role in speciation. It is one in a series of articles that will contribute to the Catalogue of Vascular Plants of Madagascar Project of the Missouri Botanical Garden (Phillipson et al., 2006; Madagascar Catalogue, 2010).

Madagascar is considered to be among the world's most critical biodiversity hotspots, and is thus a global priority for conservation (Myers et al., 2000). It has currently one of the world's highest rates of humid tropical forest deforestation (Achard et al., 2002; Brooks et al., 2002). Successful conservation strategies are dependent on sound taxonomy that provides critical data on threatened and endangered species. These data enable areas of high plant diversity and endemism to be identified, and serve to focus conservation efforts on priority targets (Hunter & Webb, 2002; Callmander et al., 2005, 2007). However, new taxonomic revisions are required for many plant groups in Madagascar, because the available treatments are based on old data and outdated species concepts and are inevitably misleading. Our revision of *Gouania* provides a good example of this, providing a very different vision of biodiversity patterns and conservation priorities for the genus than is available from existing literature. Furthermore, we have provided conservation assessments for all species (at least for their primary country of occurrence, and provided information on the known occurrence of each species in a protected area (PA). It is important to note that the PA network is currently in a state of flux in Madagascar, with the addition of new sites to the network and an increase in the total surface area of certain existing sites. Furthermore, changes are being made to the protection status of some sites; for example, numerous former Réserves Naturelles Intégrales are now classified as National Parks. Up-to-date information about the the PAs in Madagascar and their current

status can be obtained from the web site of Madagascar National Parks (2010).

Morphology of *Gouania*

The morphological characters that have been used in previous treatments of *Gouania* (notably Perrier de la Bâthie, 1943) have formed a firm foundation for our work. However, coupled with these are new observations made in the herbarium and in the field. Patterns of morphological variation and ecogeographic distribution were compared in order to circumscribe what we believe are biologically coherent taxa. A detailed discussion of the important morphological characters is given below. A key to the species allowing the determination of either flowering or fruiting specimens is provided.

LEAVES AND STIPULES

Perrier de la Bâthie (1943, 1950) placed considerable emphasis on leaf morphology. We have investigated this in greater detail and conclude that variation in leaf shape, texture, color (in dried specimens), margin type, the abaxial surface indument, and type of venation are particularly important. Most species of *Gouania* have ovate leaves, but exceptions include: *G. callmanderi* Buerki (elliptic to ovate-elliptic), *G. humbertii* H. Perrier (orbicular), *G. mauritiana* (lanceolate to deltoid), and *G. laxiflora* Tul. (cordate). The majority of the species have subcoriaceous leaf blades, but *G. cupreifolia* Buerki, Phillipson & Callm. has distinctly thicker, more rigid coriaceous blades, while *G. zebrifolia* Buerki, Phillipson & Callm. has thinner, more flexible membranous blades. Leaves of most species are more or less concolorous when dried but are notably discolorous in others (e.g., *G. phillipsonii* Buerki). Leaf margins are generally entire, but some taxa have denticulate (*G. ambrensis* Buerki, Phillipson & Callm.) or serrate (*G. mauritiana*) margins. The abaxial surface of immature leaves usually possesses some kind of indument, but this is often caducous, giving rise to glabrous mature leaves. In other species the indument is persistent and sometimes very dense, variously distributed and composed of trichomes that differ in color, length, and orientation. The presence of strong tertiary veins arising from the secondary veins is also a valuable taxonomic character. Most of the species have at least one well-developed tertiary vein arising from the lowest pair of secondary veins (in addition to the fine reticulate network of tertiary veins that is present throughout the leaf), whereas only two species (*G. humbertii* and *G. lineata* Tul.) completely and consistently lack conspicuous tertiary veins. Among all the taxa present in the region, *G. taolagnarensis* Buerki, Phillipson & Callm. has particularly well-developed venation, with even some conspicuous quaternary veins present arising from the first pair of tertiary veins. In this species the venation is more developed on one side of the leaf, causing the leaf base to be asymmetric. The reticulation is noticeably scalariform in most species; however, this pattern is inconspicuous in some taxa (e.g., *G. pannigera* Tul.). A dark brown triangular marking at the base of the stipule has been noted only in *G. ambrensis*.

FLOWERS AND INFLORESCENCE

Perrier de la Bâthie (1943) made extensive use of the shape of the hypanthium and the form of the nectary disc in delimiting taxon. Our studies confirm the importance of these characters and have revealed other variations in these organs of which Perrier de la Bâthie was apparently unaware, that we believe are also taxonomically useful. Most species have an obconic hypanthium, but *Gouania cupuliflora* Buerki, Phillipson & Callm., *G. gautieri* Buerki, Phillipson & Callm., and *G. humbertii* have a cupulate hypanthium. The nectar disc is always lobed, but the relative length of the lobes is highly variable. At one extreme, short lobes occur in *G. aphrodes* Tul. that reach only about one sixth of the length of the sepals, and at the other extreme the lobes of *G. laxiflora* are as long as or longer than the sepals. Moreover, the lobes of the disc within a single flower are markedly unequal in length in *G. scandens* (Gaertn.) R. B. Drumm. subsp. *glandulosa* (Boivin ex Tul.) Buerki, Phillipson & Callm. All species appear to have 3-lobed stigmas except those of *G. cupuliflora*, which are 2-lobed. The flowers may be sessile or pedicellate and grouped in either sessile or pedunculate glomerules, and the indument of the peduncles and pedicels is variable.

INFRUCTESCENCE AND FRUITS

In this study, several characters based on the infructescence were used to circumscribe taxa, notably the distribution of the fruits that develop to maturity, the type and color of the fruit indument, and the immature fruit shape. In most species, the fruits are equally distributed along the infructescence (e.g., *Gouania ambrensis*, *G. gautieri*), whereas in *G. perrieri* Buerki, Phillipson & Callm. they are often aggregated in the proximal part and in *G. laxiflora* they are concentrated in the distal part. Furthermore, *G. laxiflora* is the only species having a pyriform

immature fruit; the others have globose immature fruits. The indument color of the fruits may change at maturity. This is the case in *G. pannigera*, for instance, which has whitish trichomes that become reddish, and in *G. phillipsonii*, which has pale yellow to orange trichomes that become brown. In some species, for example *G. mauritiana*, the fruit indument is caducous. Unfortunately, the fruit morphology is inadequately known for several taxa, for example only mature fruits of *G. cupreifolia* and only immature fruits of *G. zebrifolia* are known.

Materials and Methods

We have examined all available material of *Gouania* at G, K, MO, P, TAN, TEF, TUB, and WAG (herbarium acronyms follow Holmgren et al., 1990), representing in total more than 550 collections. Many of the species have been observed and collected by the authors in the field. Older herbarium collections lacking geographic coordinates were post facto georeferenced as far as possible using the "Gazetteer to Malagasy Botanical Collecting Localities" (Schatz & Lescot, 2005) and other sources, and these data are surrounded by square brackets in the citation of material examined in the taxonomic treatment that follows. Species distribution maps were created using ESRI ArcView 3.3 (Redlands, California, U.S.A.). Distributions were mapped on the five bioclimatic zones of Madagascar (after Cornet, 1974; modified by Schatz, 2000). The conservation status of each species was assessed using the current IUCN Red List Categories and Criteria version 3.1 (2001). The area of occupancy (AOO), extent of occurrence (EOO; based on a grid cell size of 3 × 3 km), and calculations of the number of subpopulation are based on methods presented in Callmander et al. (2007).

Taxonomic Treatment

Gouania Jacq., Select. Stirp. Amer. Hist. 263. 1763. TYPE: *Gouania tomentosa* Jacq., Select. Stirp. Amer. Hist. 263. 1763 (lectotype, designated by Pfeiffer [1871–1875: 1488]).

Woody lianas to 20 m; stems pale to dark green, drying gray, brown, ferruginous, or blackish, with ± 6 paler ridges, glabrous or pubescent; lateral branches terminating in a spikelike inflorescence, often producing a coiled tendril in the axil of the upper leaf; stipules glabrous to densely pubescent, usually ± caducous; tendrils puberulous to villous, sometimes glabrescent. Leaves cordate to orbicular, blade subcoriaceous, rarely coriaceous (*Gouania cupreifolia*), sometimes rather membranous (*G. gautieri*, *G. zebrifolia*), petiolate; secondary veins alternate, often reaching the margin or curving upward and adjacent; conspicuous tertiary veins usually present (lacking in *G. humbertii* and *G. lineata*), arising along the lower edge of the lower secondary veins usually, conspicuous quaternary veins also present in *G. taolagnarensis*; scalariform reticulation usually visible; abaxial surface glabrous to densely pubescent, generally longer trichomes on the veins; midrib, secondary veins, and tertiary veins usually prominent; adaxial surface generally darker than the abaxial surface, glabrous to densely pubescent, venation not prominent; margin entire or toothed, flat or slightly recurved; base rounded to cordate; apex acute to rounded; glands present at the top of the petiole on the upper surface, at the base of the upper surface of the blade, and on marginal teeth. Inflorescences lax or congested, consisting of glomerules subtended by stipulelike bracts, flowers usually developing ± synchronously throughout the inflorescence; glomerules sessile or pedunculate, 3- to 20-flowered; bracts triangular or sometimes triangular-lanceolate or lanceolate, small, glabrous to densely pubescent, mostly caducous; flowers shortly pedicellate or sessile, pedicels glabrous or pubescent. Hypanthium most often obconic but occasionally cupulate; sepals 5, triangular, outer lamina generally pubescent, inner surface glabrous; petals 5, clawed, expanded section wrapped around the immature stamen; stamens 5, generally slightly longer than the petal blades, with a pale yellow filament and a pale yellow, globose anther; disc flat, 5-lobed; lobes alternating with the sepals, emarginate or somewhat truncate, very short to as long as sepals (sometimes variable in a single flower); stigma usually with 3 linear lobes, but occasionally 2-lobed (*G. cupuliflora*), style protruding from the disc. Infructescence lax or congested, bearing few to many fertile glomerules, with few to many sterile glomerules often also present. Fruits a dry 3-seeded schizocarp, globose when immature, 3-winged at maturity, dehiscing from the base into 3 valves; usually deeply emarginate at the apex and cordate at the base; seeds pale or dark brown, shiny, ovoid and slightly flattened on the inner surface, rounded on the outer surface.

Key to the Species of *Gouania* in Madagascar and the Western Indian Ocean Islands

1. Secondary veins simple, unbranched; prominent tertiary veins absent (tertiary veins comprising only a fine tertiary reticulum); both surfaces of the leaves completely glabrous 2
1′. Secondary veins branched, at least the basal pair giving rise to 1 or more prominent and conspicuous tertiary veins; adaxial surface of young leaves pubescent, at least on the veins 3

2. Leaf blades ovate to elliptic, not usually conduplicate, with 6 to 7 pairs of secondary veins; hypanthium obconic; lobes of the disc as long as the sepals; widespread in western Madagascar ..... 9. *G. lineata*
2′. Leaf blades orbicular, often conduplicate, with 4 to 5 pairs of secondary veins; hypanthium cupulate; lobes of the disc 2/3 or as long as the sepals; confined to Analamerana and Daraina (northwestern Madagascar) ..... 7. *G. humbertii*
3. Glomerules all clearly pedunculate at flowering and fruiting time; peduncles more than 1.5 mm long 4
3′. Glomerules mostly sessile or shortly pedunculate at flowering and fruiting time; peduncles mostly less than 1 mm (sometimes the basal glomerules have longer peduncles). Note that in *G. ambrensis* and *G. callmanderi* the pedicels, but not the peduncles, are relatively long (2–5 mm) 7
4. Inflorescence axes (1.5–)2 mm diam., with a brown or a reddish indument 5
4′. Inflorescence axes to 1 mm diam., puberulous or glabrescent with a whitish indument 6
5. Leaf elliptic or ovate, concolorous, glabrous on both surfaces, margin entire; hypanthium cupulate; lobes of the disc 2/3 as long as the sepals; fruits oblong (ca. 1.5 × 1 cm); seeds 7 × 4 × 0.5 mm; confined to secondary forests near Manongarivo (northwestern Madagascar)... 6. *G. gautieri*
5′. Leaf broadly ovate, discolorous, abaxial surface densely pubescent with a reddish indument, margin sparsely denticulate; hypanthium obconic; lobes of the disc 1/4 as long as the sepals; fruits spheroid (ca. 0.8 × 0.8 cm); seeds 3 × 2 × 1 mm; widespread in mid-elevation humid forest in eastern Madagascar ..... 14. *G. phillipsonii*
6. Abaxial surface of young leaf glabrous on the secondary veins and midrib; leaf margin shallowly crenate; lobes of the disc emarginate, 1/3 as long as the sepals; immature fruits winged; northwestern Madagascar (Sambirano region and Ankarana) ..... 13. *G. perrieri*
6′. Abaxial surface of young leaf puberulent; leaf margin denticulate; lobes of the disc rounded, as long as or longer than the sepals; immature fruits pyriform, unwinged at first, the wings developing late during maturation; widespread in western and southwestern Madagascar, also on Mayotte, Aldabra, and Rodrigues ..... 8. *G. laxiflora*
7. Leaf abaxially glabrous to sparsely hirsute with buff to ferruginous trichomes on veins; mature stems glabrous 8
7′. Leaf abaxially densely pubescent to villous with a whitish, grayish, or beige indument covering the limb and veins; mature stems with an evident indument 10
8. Infructescence congested; fruits small, spheroid (ca. 0.6 × 0.6 cm); lobes of the disc 1/6 as long as the sepals; leaves somewhat discolorous, tending to dry dark brown adaxially; widespread in eastern Madagascar ..... 11. *G. myriocarpa*
8′. Infructescence lax; fruits large, oblong (ca. 1 × 0.7 cm); lobes of disc more than 1/3 as long as the sepals; leaves hardly discolorous, tending to dry greenish on both surfaces; Madagascar, Comoro Islands, Mauritius, and Réunion Island ... 9
9. Lobes of the disc 1/4 to 2/3 as long as the sepals, often very variable on the same flower; fruits large, markedly wider than long (1–1.5 × ca. 2 cm), glabrous, concentrated on the distal part of the infructescence; pedicels of immature fruits often arcuate; stems and petioles dark brown; widespread in low to mid-elevation forest (0–1100 m) in eastern Madagascar, and in Mauritius ..... 15. *G. scandens*
9′. Lobes of the disc 2/3 as long or as long as the sepals; fruits small, slightly wider than long (ca. 1 × 0.7 cm), pubescent with brown trichomes, sparsely distributed over the infructescence; pedicels of immature fruits not arcuate; stems and petioles gray; from scattered localities in mid- to high-elevation forest (800–1400 m) in eastern Madagascar ..... 4. *G. cupreifolia*
10. Leaf blades orbicular or reniform, membranous, pubescent with white trichomes between the veins and brown trichomes on the veins; reticulation conspicuous, scalariform, dark; margin crenulate; recorded only from Daraina and Sahafary (northwestern Madagascar) ..... 17. *G. zebrifolia*
10′. Leaf blades ovate or elliptic, subcoriaceous to coriaceous, pubescent not as above; reticulation inconspicuous; margin entire or sparsely denticulate; Madagascar, Comoro Islands, and Réunion Island 11
11. Flowers cupulate; lobes of the disc 2/3 as long as the sepals; flowers and fruits sessile ... 5. *G. cupuliflora*
11′. Flowers obconic; lobes of the disc up to 1/2 as long as the sepals; flowers and fruits pedicellate (sometimes shortly so) 12
12. Lobes of the disc 1/2 as long as the sepals; pedicels in flowers and fruits 3–5 mm long 13
12′. Lobes of the disc to 1/4 as long as the sepals; pedicels in flowers and fruits up to 1 mm long ... 14
13. Leaf blades ovate; inner surface of the stipule with a dark brown triangle at the base; inflorescence ± congested; immature fruits with a silvery indument; fruits slightly wider than long (ca. 1.2 × 1.4 cm), sparsely pubescent with silver trichomes; known only from Montagne d'Ambre (Madagascar) ..... 1. *G. ambrensis*
13′. Leaf blades elliptic; inner surface of the stipule without triangle on the basal part; inflorescence lax; immature fruits with a yellow indument; fruits as long as wide (ca. 0.8 × 0.8 cm), puberulous at maturity; western and southwestern Madagascar ..... 3. *G. callmanderi*
14. Fruits glabrous or glabrescent with beige trichomes at maturity; apex of leaf blade acuminate or sometimes acute 15
14′. Fruits densely pubescent with reddish or brown trichomes at maturity; apex of leaf blade rounded or subacute 16
15. Leaf blades lanceolate; veins of the abaxial surface covered with a reddish indument; tertiary veins abundant, arising from the lowest secondary veins; glomerules compact, subtended by a persistent large bract; lobes of the disc distinctly thinner than the disc, emarginate, 1/4 as long as the sepals; only known with certainty from Réunion Island ..... 10. *G. mauritiana*
15′. Leaf blades elliptic to ovate; veins of the abaxial surface covered with beige trichomes, somewhat

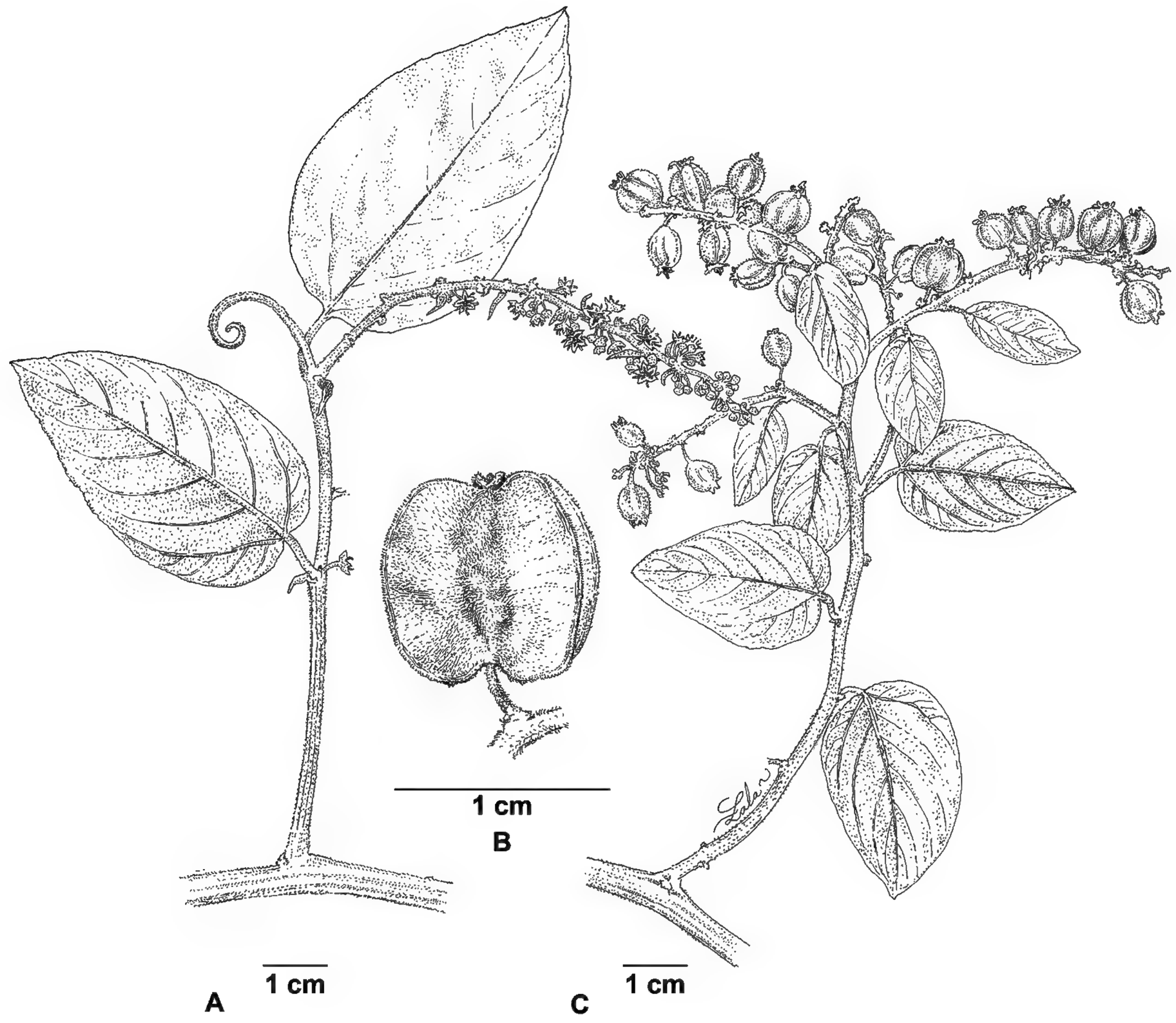


Figure 1. *Gouania ambrensis*. —A. Flowering branch, showing the disc lobes of the flowers, which reach halfway along the sepals. —B. Fruit, showing its sparse pubescence. —C. Fruiting branch, showing the even distribution of fruits throughout the infructescence. A drawn from *van Nek 1904* (TAN); B, C drawn from *van Nek 1901* (TAN).

glabrescent; tertiary veins few, arising generally from the second pair of secondary veins; glomerules lax, subtended by a caducous small bract; lobes of the disc thicker than the disc, truncate, 1/6 as long as the sepal; northern Madagascar and the Comoro Islands..... 2. *G. aphrodes*

16. Leaf blades ovate, base cordate with asymmetric lobes; leaf margin slightly crenulate near the apex; veins of the abaxial surface not reddish when dried, quaternary veins present on the larger lobe of the blade; reticulation apparent; inflorescence with a brownish indument; immature fruits covered with a yellow indument, fruits generally concentrated in the distal part of the infructescence; southeastern Madagascar (near Taolagnaro or Fort Dauphin)..... 16. *G. taolagnarensis*

16′. Leaf blades ovate, base rounded, symmetrical; leaf margin of the apex entire; veins of the abaxial surface reddish when dried, quaternary veins absent; reticulation conspicous; inflorescence with a reddish indument; immature fruits covered with a whitish indument, fruits sparsely distributed within the infructescence; central Madagascar..... 12. *G. pannigera*

1. Gouania ambrensis Buerki, Phillipson & Callm., sp. nov. TYPE: Madagascar. Antsiranana: à 7 km O du village de Bobakilandy, 12°35′17″S, 49°02′13″E, 379 m, 12 Sep. 1995 (fl.), *O. Andrianantoanina & R. Bezara 864* (holotype, MO!; isotypes, P!, TAN!). Figure 1.

Gouania mauritiana Lam. var. *latiloba* H. Perrier, Notul. Syst. (Paris) 11: 34. 1943, nom. nud.

Haec species a congeneris madagascariensibus stipulis dense pubescentibus pagina interna ad partem basalem triangulo atrofusco ornatis, foliis ovatis abaxialiter indumento lanato albido obtectis, floribus indumento argenteo vestitis, disci lobis longitudine 1/2 sepalorum partem attingentibus atque fructibus paullo latioribus quam longioribus secus infructescentiam aequaliter dispositis facile distinguitur.

Woody liana; stems dark green, drying brownish, densely pubescent with a pale brown indument on fertile shoots and with a ferruginous indument on vegetative shoots; stipules densely pubescent with a brownish indument on both surfaces, (4–)5(–6) × ca. 2 mm, inner surface with a dark brown triangular mark basally; tendrils pubescent. Leaves ovate; petioles (8–)10(–15) mm, pubescent with ferruginous or brownish trichomes; leaf blades (4–)4.5–5(–7.5) × (2–)2.5–3(–5) cm, concolorous; secondary veins alternate, 6 to

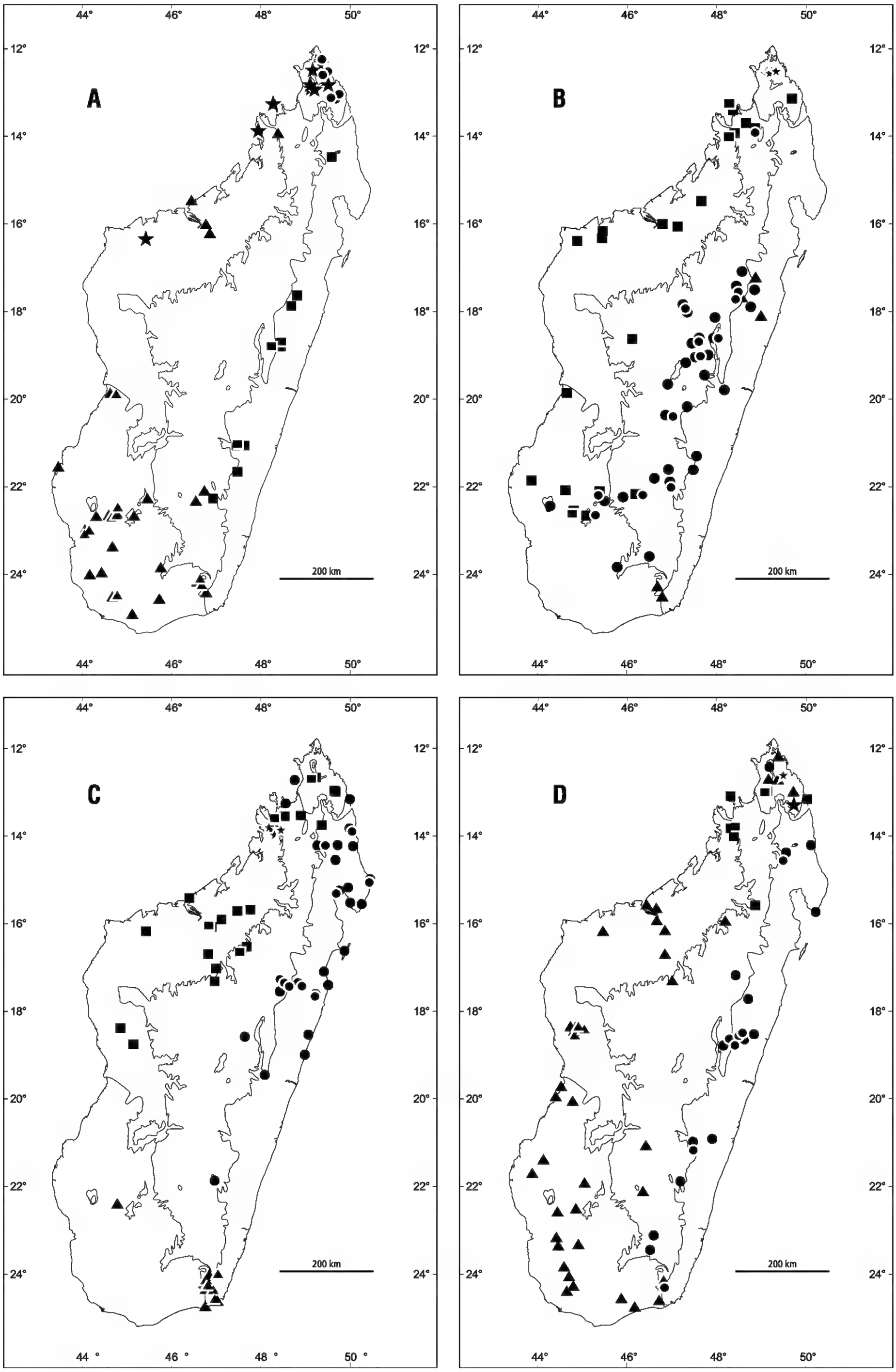


Figure 2. Distribution of *Gouania* species occurring in Madagascar, mapped on the bioclimatic zones (after Cornet, 1974; adapted by Schatz, 2000). —A. *G. callmanderi* (triangle), *G. perrieri* (star), *G. phillipsonii* (square), and *G. zebrifolia* (circle). —B. *G. ambrensis* (star), *G. cupreifolia* (triangle), *G. lineata* (square), and *G. pannigera* (circle). —C. *G. cupuliflora* (square), *G. gautieri* (star), *G. taolagnarensis* (triangle), and *G. scandens* subsp. *glandulosa* (circle). —D. *G. aphrodes* (square), *G. humbertii* (star), *G. laxiflora* (triangle), and *G. myriocarpa* (circle).

7 pairs, not reaching the margin but following it; tertiary veins apparent, 4 to 6 pairs, arising near the base of the lowest secondary veins, reticulation obscure; abaxial surface lanate with whitish trichomes; midrib, secondary veins, and tertiary veins prominent; adaxial surface pubescent with appressed whitish trichomes; margin of the young leaf blades entire, becoming sparsely denticulate with visible glands; base rounded, sometimes slightly truncate; apex generally acute, sometimes apiculate. Inflorescences ± congested, densely pubescent with a whitish indument, (5–)7–8(–12) cm, consisting of glomerules subtended by stipulelike bracts; glomerules sessile, to 10-flowered; bracts densely pubescent on both surfaces with brownish trichomes, ± persistent, (2–)3 × ca. 1 mm; flowers pedicellate, pedicels (3–)4–5 mm, densely pubescent with long silver trichomes. Hypanthium obconic, becoming subglobose as the capsule develops; sepals ca. 2 × 0.75 mm, pale yellow, outer surface densely pubescent with silver trichomes, inner surface glabrous; petals ca. 1.25 × 0.25 mm, whitish; stamens with a pale yellow filament and a pale yellow, globose, ca. 0.2 × 0.2 mm anther; disc flat, ca. 3 mm diam.; lobes ca. 1 mm, truncate or somewhat emarginate, 1/2 as long as the sepals or slightly shorter; stigma with 3 linear lobes ca. 0.25 mm, style 0.1 mm. Fruits no more than 1 developing on each glomerule, oblong (ca. 1.2 × 1.4 cm), sparsely pubescent with brown to silver trichomes, equally distributed throughout the infructescence; valves ca. 12 × 7 mm; immature fruits globose, pubescent with brown to silver trichomes; seeds pale brown, ovoid and slightly flattened, ca. 4 × 2.5 × 1 mm.

Distribution and ecology. *Gouania ambrensis* is endemic to Montagne d'Ambre in the north of Madagascar (Fig. 2B). This species grows on basement rocks in the transitional zone between humid and dry forest at an elevational range of 400 to just over 1000 m.

IUCN Red List category. *Gouania ambrensis* has an EOO of 14 km² and an AOO of 27 km², and consists of two known subpopulations, one of which occurs in a protected area. It is therefore assigned a preliminary status (IUCN, 2001) of Endangered (EN B2ab[ii]).

Phenology. This species has been collected in flower in October, with immature fruit in October and mature fruit in November.

Etymology. The epithet of the new species refers to its endemic locale, on Montagne d'Ambre in Antsiranana Province.

Discussion. Perrier de la Bâthie recognized this taxon as *Gouania mauritiana* var. *latiloba*, affiliated with *G. mauritiana* subsp. *aphrodes* (Tul.) H. Perrier, both infraspecies mentioned by him in 1943. The varietal name was not accompanied by a Latin description or diagnosis and is therefore not validly published, according to the *International Code of Botanical Nomenclature* (ICBN; McNeill et al., 2006: Art. 36.1). In this study we consider it to be a distinct species distinguished from others in the region by the combination of the following characters: ovate leaves; the presence of the dark brown, triangular mark on the basal part of the stipule inner surface (absent in all other species); the whitish indument on its inflorescence axes; the densely silvery-pubescent flowers; the lobes of its floral disc, which are one half as long as the sepals; and its mature fruits that are covered with a silver to whitish indument.

Paratypes. MADAGASCAR. **Antsiranana:** Montagne d'Ambre, versants est, 12°34′S, 49°13′E, *S. M. Trigui, M. H. Razanajatovo & S. D. Ramandimbimanana 332* (G, K, MO, P, TEF); Près d'Ambavahibe, *H. Perrier de la Bâthie 17700* (K, P); Montagne d'Ambre PA, rd. to Joffreville, 12°31′S, 49°10′E, *F. I. van Nek 1819* (TAN, WAG); Montagne d'Ambre PA, NNW of Les Roussettes, 12°28′S, 49°10′E, *F. I. van Nek 1901* (TAN, WAG); Montagne d'Ambre PA, *F. I. van Nek 1904* (TAN); Montagne d'Ambre PA, along rd. N of Joffreville, 12°29′S, 49°12′E, *F. I. van Nek 1939* (TAN, WAG).

2. Gouania aphrodes Tul., Ann. Sci. Nat., Bot. sér. 4, 8: 132. 1857, as "*Guania*." *Gouania mauritiana* Lam. subsp. *aphrodes* (Tul.) H. Perrier, Notul. Syst. (Paris) 11: 34. 1943. TYPE: Madagascar. Antsiranana: Hellville, Nov. 1847 (fr.), *L.-H. Boivin 2171* (lectotype, designated here, P!; isotype, G[2]!). Figure 3A.

Gouania eriocarpa Tul., Ann. Sci. Nat., Bot. sér. 4, 8: 133. 1857, as "*Guania*." TYPE: Comoro Islands. Grande Comore: au-dessus de Vouni, Mai 1850 (fr.), *L.-H. Boivin s.n.* (holotype, P!; isotype, G!).

Gouania pannigera Tul. f. *macrophylla* Tul., Ann. Sci. Nat., Bot. sér. 4, 8: 134. 1857, as "*Guania*" and "*macrophyllam*." TYPE: Comoro Islands. Grande Comore: au-dessus de Vouni, Mai 1850 (fr.), *L.-H. Boivin s.n.* (holotype, P!).

Woody liana; stems dark green, drying brown to ferruginous, finely pubescent to villous with somewhat caducous beige trichomes; stipules finely pubescent with beige trichomes, 2(–3) × ca. 0.75 mm; tendrils pubescent. Leaves ovate; petioles (5–)10–15(–25) mm, pubescent with beige trichomes; leaf blades (4–)5.5(–8.5) × (2–)3.5(–5) cm, discolorous; secondary veins alternate, 6 to 7(to 10) pairs, not reaching the margin but following it; tertiary veins apparent, arising

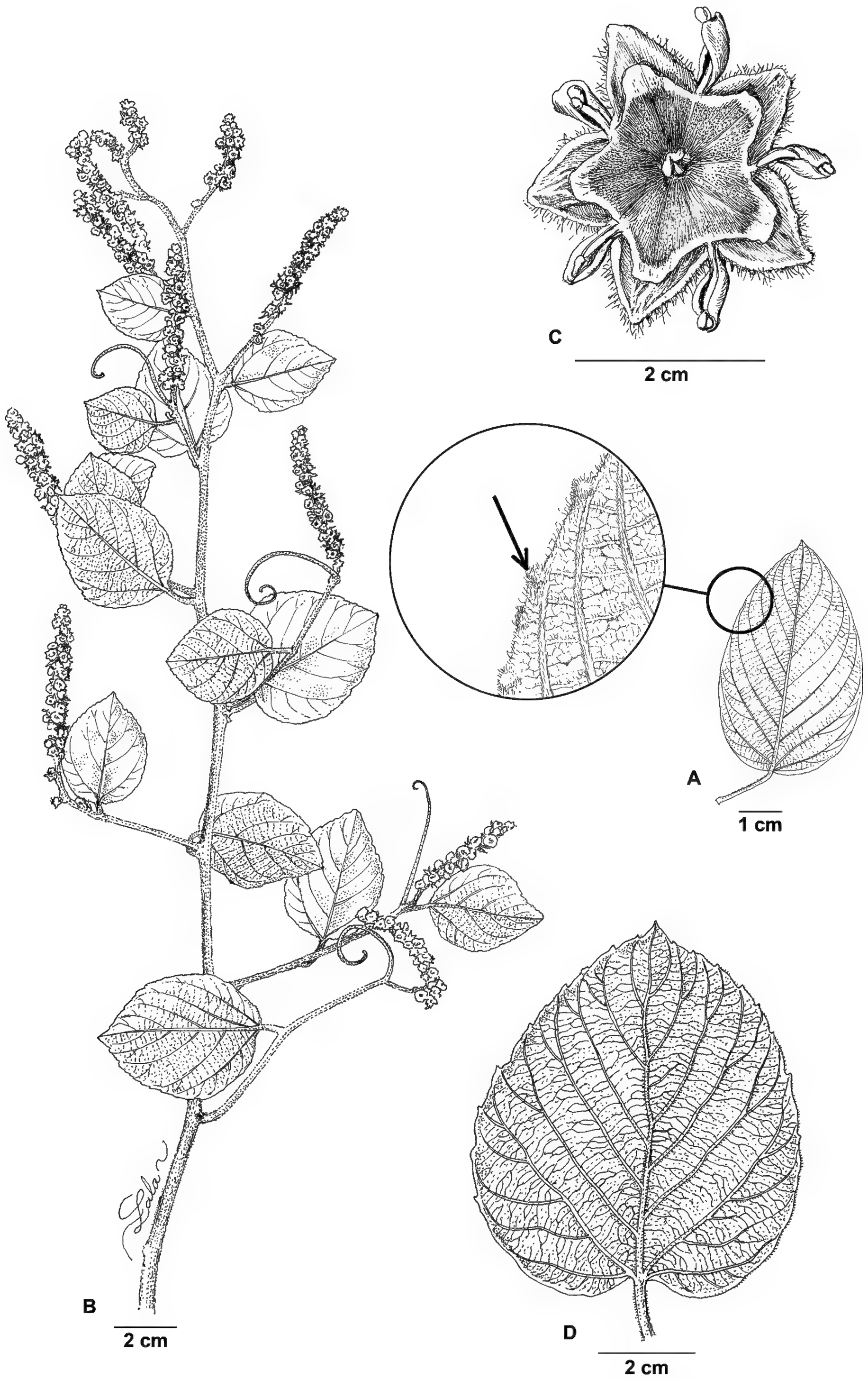


Figure 3. —A. *Gouania aphrodes*, leaf with detail of the margin. B–D. *Gouania zebrifolia*. —B. Habit. —C. Flower, showing the lobes of the disc reaching halfway along the sepals. —D. Leaf, showing its denticulate margin. A drawn from *Gentry 11892* (TAN); B–D from *Gautier et al. 4263* (TEF).

generally only from the second or third secondary veins, reticulation scalariform; abaxial surface densely pubescent to villous with beige trichomes, somewhat glabrescent (Malagasy specimens have a denser indument than those from the Comoro Islands); midrib, secondary veins, and tertiary veins slightly prominent; adaxial surface glabrescent; margin denticulate near the apex, every sinus with an apical tuft of beige trichomes; base rounded and sometimes shallowly cordate; apex acuminate. Inflorescences congested, covered with an indument similar to stems, (7–)13(–17) cm; glomerules sessile, (4 to)5- to 6-flowered; bracts densely pubescent on both surfaces with a beige indument, caducous, (2–)3 × ca. 1 mm; flowers and fruits pedicellate, pedicels to 1 mm, densely pubescent with white trichomes. Hypanthium broadly obconic, becoming subglobose as the capsule develops; sepals triangular, ca. 1.3 × 1 mm, brown to reddish when dried, outer surface densely pubescent, inner glabrous; petals ca. 1 × 0.5 mm, white; stamens slightly longer than petals, with a pale brown filament and a pale brown globose anther ca. 0.1 × 0.1 mm; disc flat, shallowly 5-lobed, ca. 3 mm diam.; lobes ca. 0.2 mm, thickened, truncate, 1/6 as long as the sepals; stigma with 3 linear lobes, those ca. 0.8 mm, style ca. 1 mm. Fruits 0 or 1 developing on each glomerule, spheroid (ca. 0.8 × 0.8 cm), glabrescent to glabrous, equally distributed throughout the infructescence; valves ca. 9 × 5 mm; seeds brown, shiny, ovoid, and slightly flattened, ca. 3 × 2 × 1 mm.

Distribution and ecology. *Gouania aphrodes* occurs in northern Madagascar and the Comoro Islands (Anjouan, Mayotte, and Mohéli) (Fig. 2D). It grows on margins of evergreen lowland forest at an elevational range from sea level to 500 m.

IUCN Red List category. Within Madagascar, *Gouania aphrodes* has an EOO of 30,560 km², an AOO of 81 km², and six known subpopulations, one of which occurs in a protected area (Manongarivo). Based on IUCN Red List criteria (IUCN, 2001), we assign a preliminary status of Vulnerable (VU B2ab[ii]) for this species in Madagascar. Its conservation status in the Comoro Islands has not been assessed.

Phenology. This species has been collected in flower in May and in fruit in August.

Discussion. *Gouania aphrodes* was based on four syntypes: *Boivin 2171*, *Boivin 2646*, *Perrillé 339*, and *Richard 133* (Tulasne, 1857). A syntype at P bears a single label with the two collection numbers *Boivin 2646* and *Richard 133* written on it; the origin of this collection is unclear and therefore would not be a suitable choice as lectotype. We select *Boivin 2171* as lectotype over *Perrillé 339*, because it is in better condition, and two duplicates are present at G.

Perrier de la Bâthie (1943) regarded this taxon as a subspecies of *Gouania mauritiana*. He also recognized two other subspecies of *G. mauritiana* from Madagascar: *G. mauritiana* subsp. *pannigera* (Tul.) H. Perrier and *G. mauritiana* subsp. *myriocarpa* (Tul.) H. Perrier. We treat these three infraspecific taxa as separate species, distinct from *G. mauritiana*. Furthermore, Perrier de la Bâthie (1943) recognized three varieties within his *G. mauritiana* subsp. *aphrodes*: the typical variety, as well as two others (*G. mauritiana* var. *angustiloba* H. Perrier, *G. mauritiana* var. *latiloba*). Neither varietal name was validly published by Perrier de la Bâthie, and in our opinion these taxa also merit recognition at the species level. They are described herein as *G. ambrensis* and *G. cupuliflora*.

Gouania aphrodes can be easily distinguished from *G. pannigera* (to which it is most similar) by its leaves, which are acuminate (vs. rounded to subacute in *G. pannigera*), having a fine, light brown indument on the abaxial surface (vs. a reddish brown indument) and denticulate margins (vs. entire or sometimes with one or two teeth near the teeth), and also by its small (ca. 0.8 × 0.8 cm), glabrescent or glabrous fruits (vs. larger, ca. 1 × 1.4 cm, sparsely reddish pubescent fruits). Furthermore, *G. aphrodes* grows in evergreen lowland forests at elevations of 0–500 m in northern Madagascar and the Comoro Islands, while *G. pannigera* colonizes the evergreen montane forests and disturbed areas at 800–1500 m in the central highlands of Madagascar.

Additional specimens examined. COMORO ISLANDS. s. loc., fr., *Boivin s.n.* (G, P); fl., *Humblot 25* (K). **Anjouan:** Anjouan, s.d., *Boivin s.n.* (P); Johanna Island, *Meller s.n.* (K). **Mayotte:** Grande Terre, Ouangani, Hachike, *Barthelat & M'Changama 428* (G, K, MO, P); Grande Terre, Ouangani, Coconi, carrefour d'Hachike, *Barthelat et al. 882* (G, K, P); s. loc., fl., *Boivin 3366* (G, K); Forêt de Mazé Mont Bini, *Humblot 1025, 1029* (P); Coconi, secondary thicket behind Director of Agriculture's residence, *Lorence 2891* (P); Sohoa, *Pascal 557* (G, K, MO, NY, P, TEF, WAG); Coconi, *Tingy 796* (P). **Mohely [Mohéli]:** inful. Mohely, s.d., *Boivin s.n.* (P); Nioumachoua, Mtrawia, *Labat et al. 3740* (G, K, MO, P). MADAGASCAR. s. loc., "Central Madagascar," fr., *Baron 302* (K); fr., *Baron 6521* (K). **Antsiranana:** Ambilobe, *Decary 14789* (P); W base of Manongarivo Massif, *Gentry 11892* (K, MO, P, TAN); A'Mananjeba (Nord), Sambirano, *Perrier de la Bâthie 6019* (P); Massif du Manongarivo, *Perrier de la Bâthie 6040* (P); Nosy Be, *Perrillé 339* (K, P); Ambonitohaka, *Réserves Naturelles 12657-RN* (TAN); Vohémar, *Richard 133* (P). **Mahajanga:** Vallée de l'Antsahakolany, *Decary 2160* (G, P); Bejofo, *Decary 2202, 2208* (P); Mandritsara, *Hb. Jard. Bot. Tananarive 16* (P); bassin moyen du Bemarivo (Boina), *Perrier de la Bâthie 6038* (P).

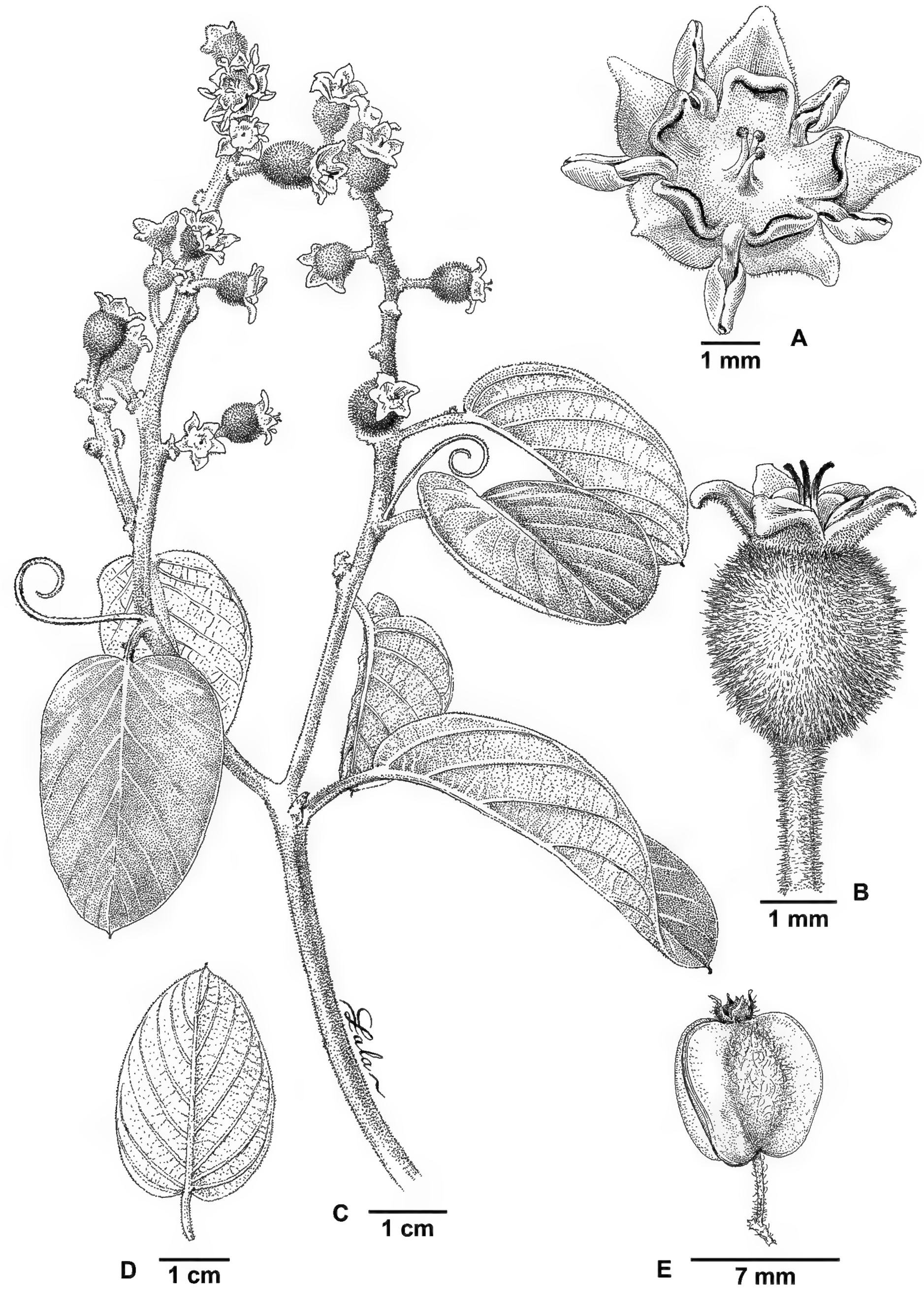


Figure 4. *Gouania callmanderi*. —A. Flower, showing the lobes of the disc reaching one fourth of the way along the sepals. —B. Immature fruit covered by a yellow indument. —C. Habit, showing the long pedicels. —D. Leaf, showing the lack of visible tertiary veins. —E. Fruit. A, D drawn from the holotype *Buerki et al. 61* (MO); B, C from *Buerki et al. 55* (TAN); E from *Bosser 28* (TAN).

3. Gouania callmanderi Buerki, sp. nov. TYPE: Madagascar. Toliara: 17 km de Sakaraha, bord de la RN7, 22°53′23″S, 44°40′43″E, 763 m, 19 Mar. 2005 (fl., imm. fr.), *S. Buerki, P. B. Phillipson & C. Rakotovao 61* (holotype, MO!; isotypes, BR!, G!, K!, P!, S!, TAN!, US!, WAG!). Figure 4.

Haec species a congeneris madagascariensibus foliis parvis ellipticis usque ovato-ellipticis abaxialiter indumento albido obtectis, floribus pedicellis longis insidentibus, disci lobis longitudine 1/4 sepalorum partem attingentibus atque fructu juvenili indumento luteo obtecto facile distinguitur.

Woody liana climbing to 8 m; stems dark green, drying brown, finely pubescent to villous with brown to whitish trichomes; stipules ca. 1 × 0.25 mm, densely villous with brown trichomes; tendrils villous or pubescent. Leaves elliptic to ovate-elliptic; petioles (9–)10(–16) mm, pubescent to villous with brown trichomes and sometimes also white trichomes; leaf blades (3.5–)4.5–5(–7) × (2–)2.5–4.5(–5) cm, discolorous; secondary veins alternate, 7 to 8 pairs, reaching and following the margin; tertiary veins apparent, 1 or 2 pairs, sometimes arising near the base of the lowest secondary vein, reticulation obscure; abaxial surface pale green, villous with white trichomes, and with occasional long brown trichomes present on the midrib and on the secondary veins, margin entire; midrib and secondary veins prominent; adaxial surface finely and sparsely villous, with longer white trichomes on veins; margin entire; base rounded; apex acute to shortly attenuate, with a short apiculus bearing a tuft of long trichomes. Inflorescences somewhat lax, pubescent with whitish trichomes, (4.5–)6–8(–14) cm, consisting of glomerules subtended by stipulelike bracts; glomerules generally pedunculate, (1–)4 mm, sometimes sessile, white-villous, 4- to 8-flowered; bracts densely pubescent on the outer surface with pale brown trichomes, glabrous on the inner surface, caducous, (1–)2 × ca. 0.5 mm; flowers apparently protandrous, borne on (2–)3(–4) mm, villous pedicels. Hypanthium broadly obconic, ca. 1 × 1.5 mm, becoming subglobose as the capsule develops; sepals ca. 1 × 1 mm, pale yellow, outer surface villous, inner glabrous; petals ca. 1 × 0.25 mm, white; stamens slightly longer than petal, with a pale yellow filament and a pale yellow anther ca. 0.3 × 0.2 mm; disc flat, ca. 3 mm diam.; lobes ca. 0.25 mm, slightly recurved, rounded to shallowly emarginate or somewhat truncate, 1/4 as long as the sepals, young disc yellow, becoming pale yellow; stigma with 3 linear lobes, those ca. 0.4 mm, style ca. 0.5 mm. Fruits 0 to 2 developing on each glomerule, small (ca. 0.8 × 0.8 cm), spheroid, puberulous, equally distributed throughout the infructescence; valves ca. 8 × 4 mm; immature fruits with a yellow indument; seeds brown, shiny, ovoid and slightly flattened, ca. 3 × 2 × 1.5 mm.

Distribution and ecology. *Gouania callmanderi* grows in western and southwestern Madagascar (Fig. 2A). The new species can be found in semi-deciduous, deciduous, and xerophytic vegetation on limestone and sand at an elevation range from sea level to 1300 m.

IUCN Red List category. With an EOO of 296,807 km², an AOO of 279 km², and 22 known subpopulations, five of which occur within protected areas (Ampijoroa, Andohahela, Isalo, Manongarivo, Zombitsy), *Gouania callmanderi* is assigned a preliminary status of Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Phenology. This species has been observed flowering from October to March and fruiting from April to August.

Etymology. The species epithet was chosen by the first author in honor of Martin W. Callmander (1975–), Swiss botanist and co-author of this article, who introduced Sven Buerki to the Malagasy flora and supervised his M.Sc. dissertation, and in appreciation of his valued collaboration on numerous projects.

Discussion. This species is closest to *Gouania ambrensis* in the length of the pedicels and the whitish color of the inflorescence indument, but differs most notably in having elliptic to ovate-elliptic, discolorous leaves (vs. ovate, concolorous in *G. ambrensis*), lobes of the disc about one fourth as long as the sepals (vs. lobes about one half as long), immature fruits with a yellow indument (vs. a brown to silver indument), and small fruits (ca. 0.8 × 0.8 cm vs. ca. 1.2 × 1.4 cm). Furthermore, *G. callmanderi* occurs throughout the west of Madagascar and is especially abundant in the southwest, whereas *G. ambrensis* is endemic to the Montagne d'Ambre in the extreme north of the island.

Paratypes. MADAGASCAR. **Antsiranana:** Manongarivo/Ambongo, [13°59′24″S, 48°22′12″E], *H. Perrier de la Bâthie 6026* (P). **Fianarantsoa:** Vestiges forestiers à l'entrée d'Ihosy, 22°18′15″S, 46°16′43″E, *S. Buerki, P. B. Phillipson & C. Rakotovao 55* (K, MO, P, TAN); Ihosy, [22°23′S, 46°07′E], *J. Peltier & M. Peltier 2725* (TAN); rd. from Ihosy to Farafangana (9 km before Ihosy), 22°33′02″S, 46°32′36″E, *P. De Block 1954* (BR, MO, P). **Mahajanga:** Antsianitia, 15°34′54″S, 46°25′14″E, *M. W. Callmander & Phillipson 687* (G, K, MO, P, TAN); Ampijoroa, 16°19′S, 46°49′E, *Phillipson 1929* (K, P, TAN, WAG); vic. of Lac Ampijoroa, [16°11′S, 47°06′E], *A. Gentry 11456* (K, MO, P, TAN, WAG), *Gentry 11487* (MO, P, TAN). **Toliara:** Forêt

de Marosalaza, 50 km N de Morondava, [20°02′S, 44°33′E], *J. P. Abraham 115 part A* (K, P); Manasoa Tanosy, *K. R. Afzelius s.n.* (P); Lambomakondra, [22°42′S, 44°42′E], *J. Bosser 28* (TAN); Masokara, plateau Mahafaly, Ankalirano, [20°02′S, 44°33′E], *Bosser 14282* (TAN); Zombitsy PA, 22°52′43″S, 44°42′51″E, *Buerki, Phillipson & Rakotovao 59* (BR, G, K, MO, P, S, TAN, US, WAG); Rte. d'Anjamala, [23°11′30″S, 43°57′30″E], *F. Chauvet 441* (P, TEF); Zombitsy PA, [22°49′48″S, 44°41′24″E], *T. B. Croat 30711* (MO, TAN); 23–43 km E of Tulear along rd. to Andranovory, [23°19′S, 43°56′E], *Croat 31027* (MO, TAN, WAG); SW of Ampanihy on rte. to Androka betw. Ambanihy & PK 10, [24°45′S, 44°41′E], *Croat 31392* (MO, TAN); Sakaraha, [22°54′S, 44°32′E], *R. Decary 14104* (P); Morombe, [21°44′S, 43°21′E], *Decary 18758* (P); Beroroha, [22°53′S, 44°14′E], *Decary 18857* (P); Lambomakandro, [22°42′S, 44°42′E], *Decary 18904* (P); Ranohira, [22°29′S, 45°24′E], *Decary 18921* (P); Environs d'Ihosy, *B. Descoings 2173* (TAN); Mandrare moyen, environs de Beza Esiva (Sud), [24°25′S, 46°32′E], *Descoings 2741* (MO, TAN); ca. 20 km W of Ampanihy on rte. to Androka, 24°46′S, 44°36′E, *D. J. Du Puy, J.-N. Labat & Phillipson MB610* (TAN); Zombitsy PA, off RN7, 22°52′S, 44°40′E, *Du Puy, Labat & B. Rakouth MB654* (TAN); Vallée de la Manambolo, (bassin du Mandrare) au NW de Maroaomby (Betsioky), [24°21′20″S, 46°34′30″E], *H. Humbert 12789* (G, P); Vallée de la Manambolo, rive droite (bassin du Mandrare) aux environs d'Isomono (confluent de la Sakamalio), [24°30′S, 46°37′E], *Humbert 12985* (K, P, TAN); haute vallée de la Menarahaka à l'Est d'Ihosy, [22°32′30″S, 46°29′50″E], *Humbert 28553* (P); Environs d'Antanimora (Androy), 30–35 km au N d'Ambia, [24°49′S, 45°40′E], *Humbert 28814* (P); SW de Betioky près du village d'Ankalirano, [24°13′S, 44°17′E], *M. Keraudren 825* (P); RN7 at 15 km NE of Sakaraha, [22°96′S, 44°36′E], *D. H. Lorence 1904* (K, MO); 54 km SW of Tulear, 23°13′S, 44°03′E, *J. S. Miller & A. Randrianasolo 6169* (K, MO, P, TAN); Zombitsy PA, [23°53′00″S 44°40′00″E] *P. Morat 680* (TAN); Plateau Mahafaly au NW d'Ejeda, [24°15′S, 44°05′S], *Morat 4344* (P, TAN); 55 km NE of Morondava via rte. 8, 20°04′S, 44°40′E, *R. D. Noyes, D. K. Harder, E. A. Rakotobe, T. G. Razafindrabeaza & J. P. Abraham 1051* (MO, P, WAG); bords de la Mahavavy/Ambongo, *Perrier de la Bâthie 6024* (P); Zombitsy PA, 22°52′S, 44°31′E, *Phillipson 3090* (K, MO, P, TAN, WAG); Ranobe Forest, 22°56′50″S, 43°41′08″E, *P. B. Phillipson, R. Ranaivojaona, N. M. Andrianjafy & R. A. Lubke 5900* (G, K, MO, P, TAN, WAG); 5 km N of Beloha on RN10 to Ampanihy, 25°07′S, 45°06′E, *P. B. Phillipson & J. R. Milijaona 3627* (G, K, MO, P, TAN, WAG); Andohaela PA, [24°40′12″S, 46°44′24″E], *Réserves Naturelles 5201* (P, TAN), *Réserves Naturelles 5949* (P, TAN); Environs d'Ampandrandava, [24°05′S, 45°42′E], *A. Seyrig 214 B* (P); Ampandrandava, *Seyrig 369* (P).

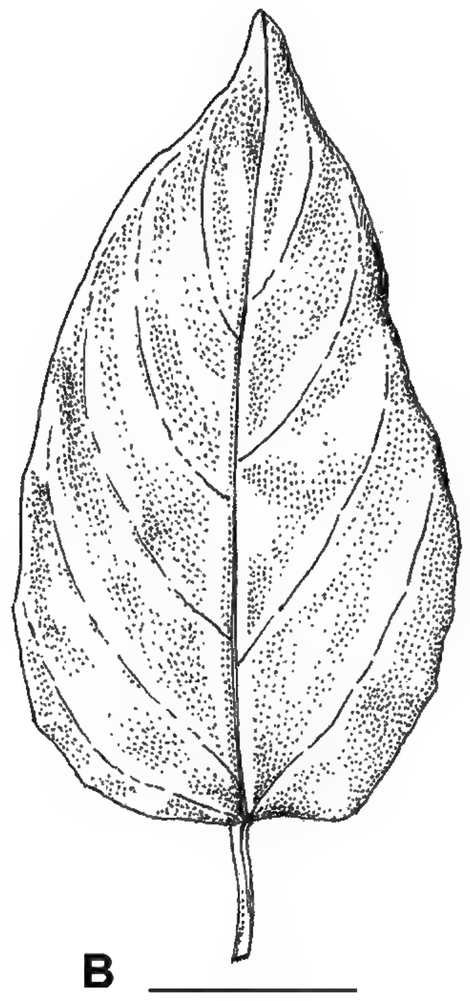
4. Gouania cupreifolia Buerki, Phillipson & Callm., sp. nov. TYPE: Madagascar. Toliara: Vallée de la Manambolo, rive droite (bassin du Mandrare) aux environs d'Isomono (confluent de la Sakamalio), Mont Morahariva (Mahamena-Marovato), 1000–1400 m, Dec. 1933 (fl.), *H. Humbert 13288* (holotype, P!; isotype, G!). Figure 5.

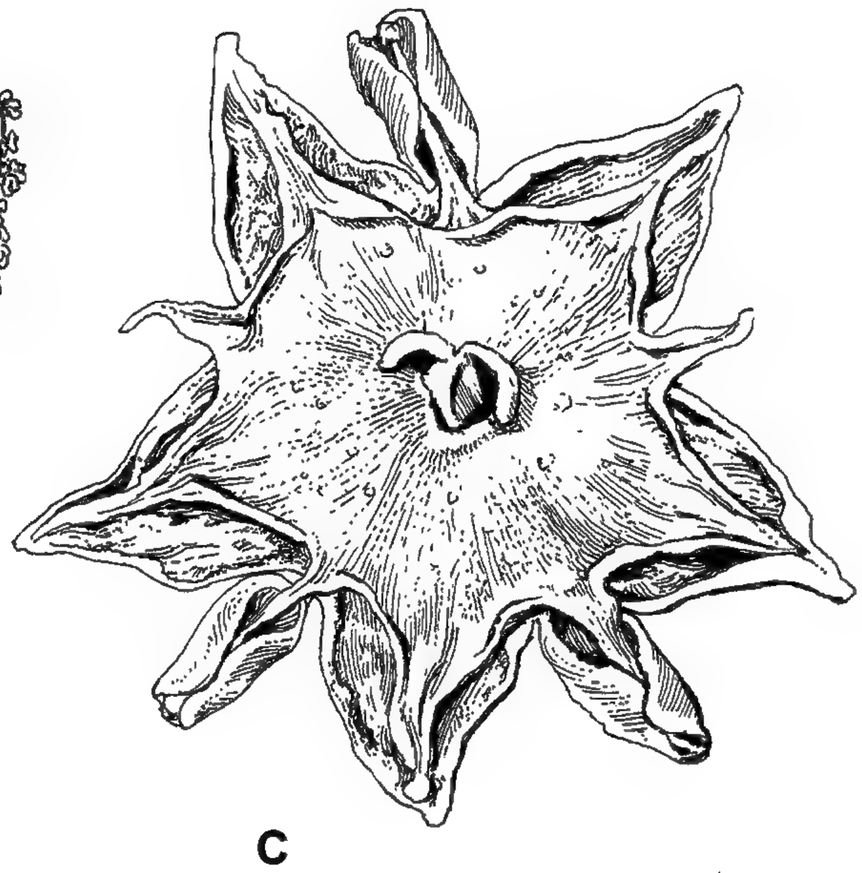
Haec species a congeneris madagascariensibus foliis in sicco abaxialiter cupreis ad marginem leviter recurvatis, disci lobis sepalis paullo brevioribus vel ea aequantibus atque fructibus parvis pubescentibus secus inflorescentiam sparsim dispositis facile distinguitur.

Woody liana climbing to 15 m; stems pale to dark green, drying gray, partially glabrescent with brown trichomes persisting on the ridges, young shoots sparsely pubescent with brown trichomes; stipules glabrate, (1–)2 × ca. 0.75 mm; tendrils pubescent. Leaves ovate, coriaceous; petioles gray, 12–15(–20) mm, sparsely pubescent with brown trichomes; leaf blades (4–)4.5–5.5(–7) × (3–)3.5(–5) cm; secondary veins alternate, 5 to 6 pairs, not reaching the margin but following it; tertiary veins apparent, arising near the base of the lowest secondary veins, sometimes absent, reticulation scalariform; abaxial surface glabrous, sparsely pubescent on the veins, a distinct coppery color when dried; midrib, secondary veins, and tertiary veins prominent; adaxial surface glabrous; margin entire, slightly recurved; base rounded to shallowly cordate; apex acute. Inflorescences ± lax, pubescent with a brownish indument, (4.5–)5.5–6(–8) cm, consisting of glomerules subtended by stipulelike bracts; glomerules sessile, shortly pedicellate, up to 1.5 mm long at the base of the inflorescence, 5- to 6-flowered; bracts small, densely pubescent on the outer surface with reddish trichomes, glabrous on the inner surface, (0.5–)1 × ca. 0.25 mm; flowers pedicellate, pedicels (1–)2 mm, covered with a whitish indument. Hypanthium obconic, becoming subglobose as the capsule develops; sepals ca. 1.25 × 0.75 mm, pale brown, outer surface sparsely pubescent, inner glabrate; petals ca. 0.75 × 0.2 mm, pale brown, sometimes yellow; stamens slightly longer than the petal blades, with a pale brownish filament and a pale yellow, globulose anther ca. 0.2 × 0.2 mm; disc flat, ca. 2 mm diam.; lobes ca. 0.8 mm, triangular-lanceolate, 2/3 or as long as the sepals; stigma with 3 linear lobes, those 5–8 mm, style ca. 3 mm. Fruits solitary on the glomerule, small, oblong (ca. 0.7 × 1 cm), pubescent with brown trichomes, scattered throughout the infructescence; valves ca. 7 × 5 mm; immature fruits not seen; seeds brown, shiny, pyriform, and slightly flattened, ca. 2.5 × 2 × 0.5 mm.

Distribution and ecology. *Gouania cupreifolia* grows on the eastern escarpment of Madagascar (Fig. 2B). It can be found in sclerophyllous and deciduous vegetation at elevations of 800–1400 m.

IUCN Red List category. With an EOO of 37,956 km², an AOO of 45 km², and only five subpopulations, two of which occur within protected areas





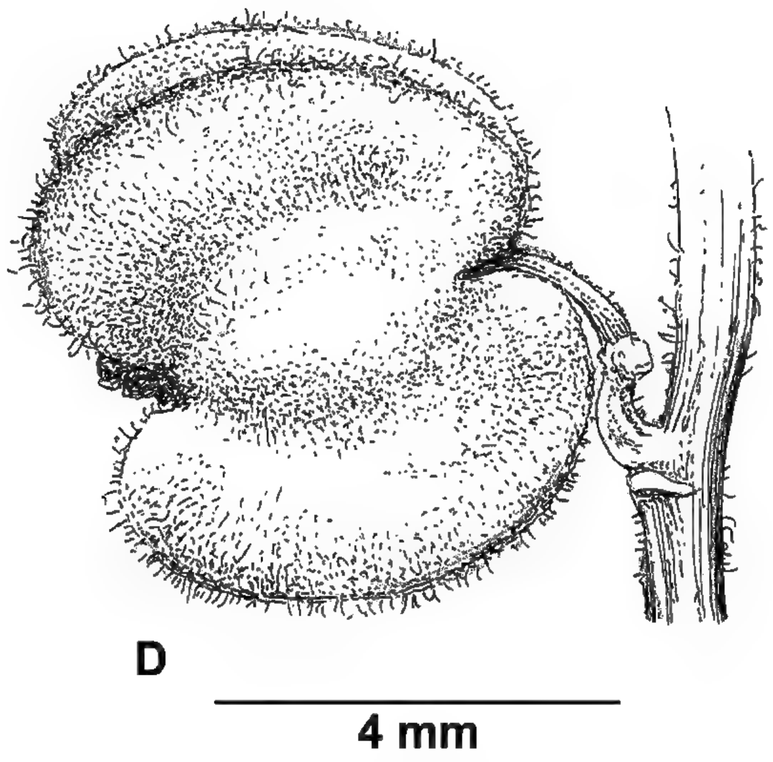


Figure 5. *Gouania cupreifolia*. —A. Habit. —B. Leaf. —C. Flower, showing the lobes of the disc slightly shorter than or as long as the sepals. —D. Fruit. A–C drawn from the type *Humbert 13288* (P); D from *Homolle 2595* (P).

(Andohahela National Park, Betampona Nature Reserve), *Gouania cupreifolia* is assigned a preliminary status of Vulnerable (VU B2ab[ii]) according to IUCN Red List criteria (IUCN, 2001).

Phenology. *Gouania cupreifolia* has been observed flowering from December to January and fruiting in January.

Etymology. The new species epithet refers to the unusual, somewhat coppery color of the undersurface of the dried leaves.

Discussion. *Gouania cupreifolia* differs from all Malagasy species by the abaxial surface of its leaves drying to an unusual, somewhat coppery color, and the slightly recurved margins of the blade. Based on floral morphology, it appears to be most closely related to *G. laxiflora*, having the lobes of the discs slightly shorter than or as long as the sepals (ca. 0.8 mm long).

Paratypes. MADAGASCAR. **Toamasina:** Ankaroka, [17°48′S, 48°32′E], *G. Cours 234* (P); Forêt d'Ankiribiry, *Cours 2598* (P); Betampona PA, Anjiro en descendant le ruisseau, Ranomena, [17°55′S, 49°13′E], *A. M. Homolle 2595* (P). **Toliara:** bassin de réception de la Mananara, affluent du Mandrare, pentes occidentales des montagnes entre l'Andohahela et l'Elakelaka, mont Apiky au-dessus de Mahamavo, [24°45′30″S, 46°43′30″E], *H. Humbert 13855* (P); Ampandrandava, [24°05′S, 45°42′E], *A. Seyrig 369* (P), *369 bis* (P).

5. Gouania cupuliflora Buerki, Phillipson & Callm., sp. nov. TYPE: Madagascar. Antsiranana: Ambanja, Ramena River, Chute d'Ambobaka, 13°44′48″S, 48°31′37″E, 40 m, 28 Feb. 2005 (fl.), *S. Buerki & S. Wohlhauser 29* (holotype, MO!; isotypes, G!, K!, P!, TEF!). Figure 6D–G.

Gouania mauritiana Lam. var. *angustiloba* H. Perrier, Notul. Syst. (Paris) 11: 34. 1943, nom. nud.

Haec species a congeneris madagascariensibus glomerulis sessilibus inter se distantibus ex floribus sessilibus cupulatis constantibus, disci lobis longitudine 2/3 sepalorum partes attingentibus, stigmatis lobis duobus linearibus atque fructu oblongo pubescente facile distinguitur.

Woody liana climbing to 3 m; stems dark green, drying blackish, densely pubescent with hirsute ferruginous trichomes; stipules densely pubescent with reddish brown trichomes, 2–3(–4) × ca. 0.75 mm; tendrils pubescent. Leaves ovate; petioles (5–)10–15(–20) mm, pubescent with ferruginous trichomes; leaf blades (3.5–)5.5(–6) × (1.5–)3 cm; secondary veins alternate, 7 to 9 pairs, reaching and following the margin; tertiary veins apparent, arising near the base of the lowest secondary veins, reticulation scalariform; abaxial surface sparsely pubescent with white trichomes; midrib, secondary veins, and tertiary veins prominent; adaxial surface sparsely pubescent with a fine white indument; margin entire; base rounded; apex acute to shortly attenuate. Inflorescences lax, pubescent with a brownish indument, (7–)11(–15) cm, consisting of well-spaced glomerules subtended by stipulelike bracts; glomerules sessile or shortly pedunculate, (3 to)8-flowered; bracts small, densely pubescent on the outer surface with a brownish indument, glabrous on the inner surface, caducous, (1–)2 × ca. 0.5 mm; flowers sessile, with a reddish indument. Hypanthium cupulate; sepals ca. 0.8 × 1 mm, whitish to pale yellow, the outer surface densely pubescent with reddish trichomes, the inner glabrous; petals ca. 1 × 0.5 mm, white; stamens slightly longer than the petal blades, with a pale yellow filament and a pale yellow, globulose anther ca. 0.2 × 0.2 mm; disc flat, ca. 3 mm diam.; lobes ca. 0.5 mm, emarginate or somewhat truncate, 2/3 as long as the sepals; stigma with 2 linear lobes, ca. 0.2 mm, style ca. 0.4 mm. Fruits 0 or 1 developing on each glomerule, oblong, ca. 1.1 × 1 cm, pubescent to puberulent with a brownish indument, equally distributed throughout the infructescence; valves ca. 10 × 4 mm, shallowly emarginate at the apex and the base; immature fruits globose, with a dense, pale yellow indument; seeds brown, shiny, ovoid and slightly flattened, ca. 5 × 3 × 1 mm.

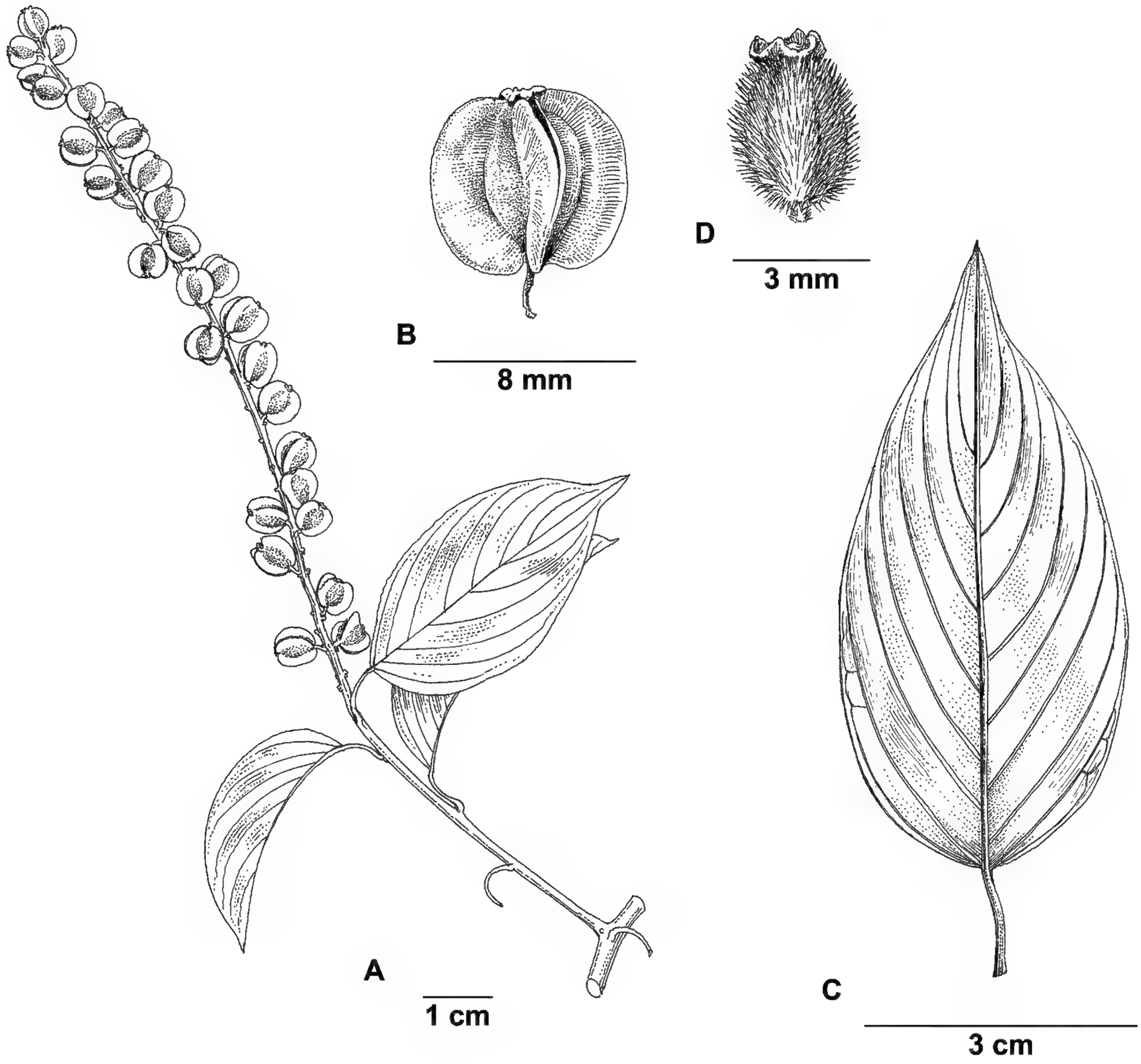
Distribution and ecology. Endemic to northwestern Madagascar (Fig. 2C), *Gouania cupuliflora* occurs on sandy substrates and on limestone at elevations between 30 and 500 m, mainly in evergreen lowland rainforest, or in dry forest along rivers.

IUCN Red List category. *Gouania cupuliflora* has an EOO of 121,012 km² and an AOO of 207 km², with 20 known subpopulations, six of which occur within protected areas (Ampijoroa, Ankarafantsika, Ankarana, Bemaraha, Manongarivo, Namoroka). It is thus assigned a preliminary status of Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Phenology. *Gouania cupuliflora* has been observed in flower from January to April and in fruit from May to November.

Etymology. The new species is named for its markedly cupulate flowers.

Discussion. Perrier de la Bâthie referred material of this species to *Gouania mauritiana* var. *angustiloba* in his 1943 revision for the family (mentioned under *G. mauritiana* subsp. *aphrodes*). The varietal name was not accompanied by a Latin description or diagnosis and is therefore not validly published,



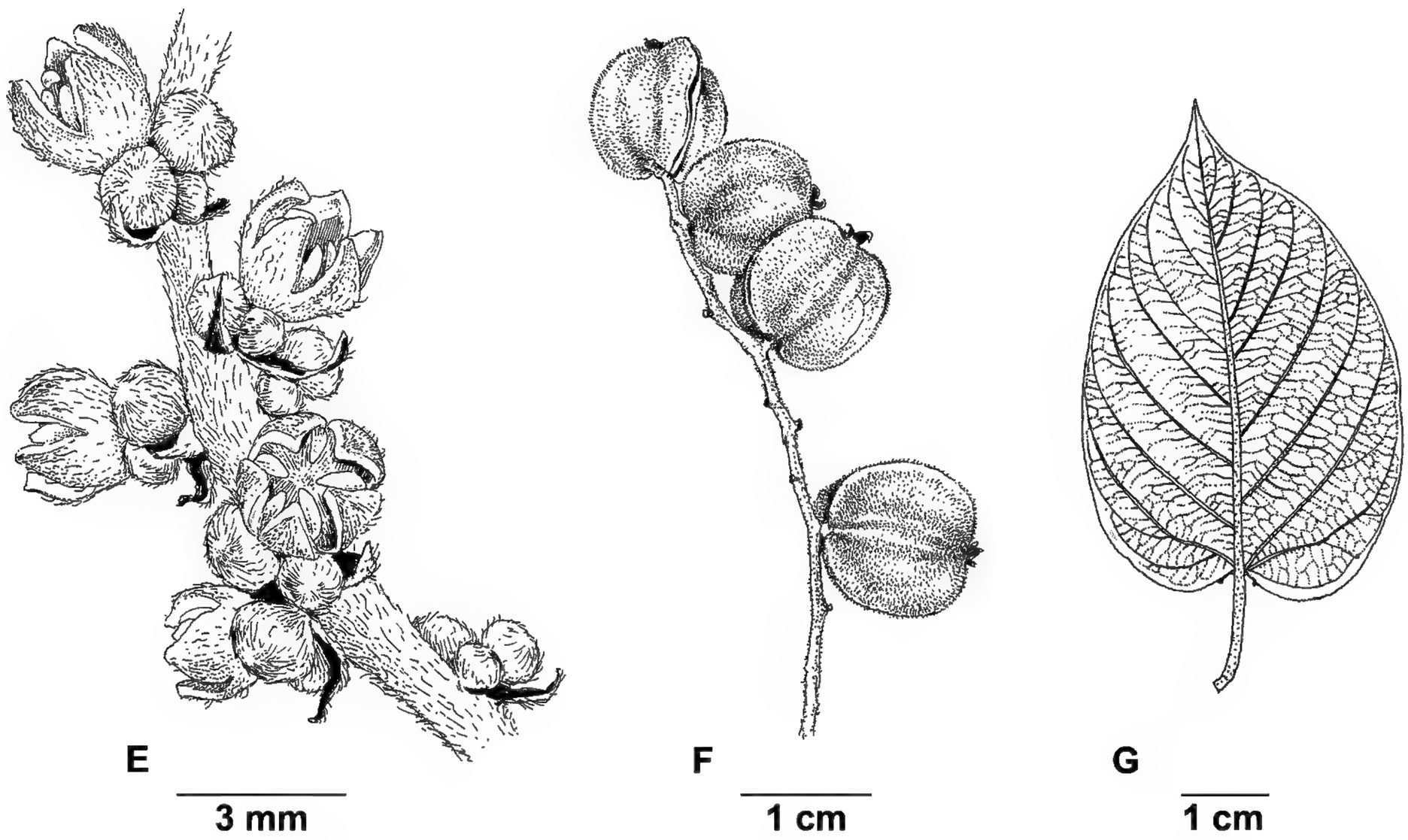


Figure 6. A–C *Gouania lineata*. —A. Fruiting branch showing the dense infructescence of small fruits. —B. Fruit. —C. Leaf showing the lack of conspicuous tertiary veins. D–G. *Gouania cupuliflora*. —D. Young pyriform fruit. —E. Inflorescence showing the sessile glomerules composed of sessile cupulate flowers, and the lobes of the disc reaching two thirds the length of the sepals. —F. Infructescence. —G. Leaf, abaxial surface. A drawn from *Morat 4454* (TAN); B, C from *Gentry 11471* (TAN); D from *Perrier de la Bâthie 6015* (TAN); E from the holotype *Buerki & Wohlhauser 29* (MO); F, G from *Derleth 62* (TAN).

according to the ICBN (McNeill et al., 2006: Art. 36.1). The varietal epithet chosen by Perrier de la Bâthie (1943) refers to narrow lobes of the disc relative to the other elements he included in *G. mauritiana*, but this name is not particularly appropriate in the context of the genus as a whole. We regard the taxon as a distinct species that we name *G. cupuliflora* in reference to its cupulate hypanthium. *Gouania cupuliflora* is allied to *G. ambrensis*, but differs by its sessile flowers covered outside by a ferruginous indument (vs. pedicellate flowers covered by silver trichomes in *G. ambrensis*), the cupulate hypanthium (vs. obconic hypanthium), the lobes of the disc reaching two thirds as long as the sepals (vs. lobes of the disc reaching one half of the sepals), and the stigma with two linear lobes (vs. the stigma 3-lobed).

Paratypes. MADAGASCAR. s. loc., fl., *R. Baron 4680* (K, P); fl., *R. Rakoto 18* (TAN); fl., *Service Forestier 13* (P). **Antsiranana:** Ankarana, *M. Bardot-Vaucaulon 1537* (K, MO, P, TAN); Chute d'Ambobaka, affluent de la Ramena, 13°44′50″S, 48°31′36″E, *M. W. Callmander 286* (G, K, MO, P, TEF); entre Vohémar et Ambilobe, *R. Decary 14659* (P); Besinkara, chemin d'Ambodisakoana à Ambalafary, *P. Derleth 62* (G, K, MO, P, TAN); Daraina, forêt d'Ambilondomba, 13°10′S, 49°39′E, *L. Gautier 4269* (G); Besinkara, Ambalafary, 14°04′S, 48°17′E, *Gautier & S. T. Be 2883* (G, K, TAN, TEF); 3–5 km E of Diego-Suarez-Ambilobe Rd., 7 km N of Ambilobe, [13°11′30″S, 49°03′30″E], *A. Gentry 11917* (MO, P, TAN); Ankarana PA, ca. 5 km NW of Park Village near Besaboba Stream, 12°51′16″S, 49°17′30″E, *D. K. Harder, M. C. Merello, S. G. Razafimandimbison & T. G. Razafinfrabaeza 1762* (MO, P, TAN, WAG); Tsaratanana, région O de Majunga, *R. P. Heydel s.n.* (P); Vallée de Sambirano, *H. Perrier de la Bâthie 6015* (P, TAN); Ambohimarina, plaine du Sambirano, 13°54′21″S, 48°29′21″E, *Wohlhauser 60006* (G, TEF); Bassin versant de rano Bemahalegny, moyen Ambahatra, cours moyen du bassin-versant rano Ambahatra, 13°57′51″S, 48°26′56″E, *Wohlhauser 60046* (G, MO, TEF). **Mahajanga:** Analafaly, Fokontany Bemanevika, Analafaly forest, 6 km E of Marotaolana, 17°13′10″S, 46°59′42″E, *C. Birkinshaw & N. M. Andrianjafy 1500* (MO, P, TAN); Ouest environs de Maevatanana, près d'Ambodiroka, pont de la Betsiboka, [17°01′S, 47°45′E], *B. Descoings 3301* (TAN); Ampijoroa STF, ca. 3 km N d'Andranofasika, 16°20′S, 46°51′E, *L. G. Dorr & L. Koenders 3014* (K, P, TAN, WAG); Mailaka, région du Cap St. André, *H. L. Douillot s.n.* (P); Bemaraha massif, base of escarpment, ca. 10 km W of Marerano on Manambolo River, 19°04′S, 45°04′E, *B. Du Puy, D. Du Puy, J. Andrianatina & B. Carlson MB730* (MO, P, TAN); Ampijoroa, 16°19′S, 46°49′E, *Gentry & G. E. Schatz 62101* (TAN); Vallée de la Betsiboka, en amont de Maevatanana, [16°57′S, 46°50′E], *H. Humbert 4442 bis* (P); 10 km E Antsalova, at edge of the Tsingy of Bemaraha, [18°39′S, 44°37′E], *J. Klackenberg 93.03.11–9* (MO, P); Bemaraha PA, [18°39′S, 44°37′E], *J. D. Leandri 861* (P); Ambodiriana (Antsiafabositra), [15°55′S, 47°29′E], *J. Peltier & M. Peltier 5183* (P); Amborovy, [15°39′30″S, 46°20′30″E], *Peltier & Peltier 5297* (P); Morofotra, rive gauche de l'Ikopa en face de Maevatanana, *Perrier de la Bâthie 6025* (P); moyen bassin du Bemarivo, Boina, [15°55′S, 47°40′E], *Perrier de la Bâthie 6045* (P); Ampasimatera, bassin moyen de Bemarivo (Boina), [15°56′S, 47°44′E], *Perrier de la Bâthie 6052* (P); Boina, *Perrier de la Bâthie 14647* (P, TAN); Marosakoana, *Réserves Naturelles 5* (P); Namoroka PA, [16°29′S, 45°22′E], *Réserves Naturelles 5094* (P), *Réserves Naturelles 6385* (P, TAN), *Réserves Naturelles 6416* (P, TAN); Canton Andranomavo, distr. Soalala, *Réserves Naturelles (Randriamera) 10144* (P, TEF); Ankarafantsika PA, *Service Forestier 6* (P); Ampijoroa, [16°18′S, 46°49′E], *Service Forestier 29760* (TEF).

6. Gouania gautieri Buerki, Phillipson & Callm., sp. nov. TYPE: Madagascar. Antsiranana: Besinkara, chemin entre Ambalafary et Ambodisakoana, 14°04′S, 48°17′E, 350 m, 26 Mar. 1996 (fl.), *L. Gautier & S. T. Be 2904* (holotype, G!; isotypes, K!, P!, TAN!, TEF!). Figure 7.

Haec species a congeneris madagascariensibus foliis glabris membranaceis ellipticis usque ovatis, inflorescentia trichomatibus brunneis hirsuta, glomerulorum pedunculis saepe dichotomis, floribus cupulatis subsessilibus, disci lobis longitudine 2/3 sepalorum partes attingentibus, fructu magno trichomatibus brunneis hirsuto atque semine ovoideo pallide brunneo facile distinguitur.

Woody liana climbing to 8 m; stems dark green, drying dark green to gray, glabrescent, young shoots pubescent, with brown trichomes; stipules glabrous, 2(–3) × ca. 0.75 mm; tendrils glabrescent. Leaves elliptic to ovate, blade rather membranous; petioles (7–)10–12(–20) mm, glabrous; leaf blades (5.5–)6.5–7(–11) × (2–)3.5(–5.5) cm; secondary veins alternately arranged, 4 to 5 pairs, not reaching the margin but following it; tertiary veins apparent, arising near the base of the lowest secondary veins, reticulation scalariform; abaxial surface glabrous; midrib, secondary veins, and tertiary veins slightly prominent; adaxial surface glabrous; margin entire; base rounded; apex acute. Inflorescences lax, (3–)4–5(–8) cm, pubescent with brown hirsute trichomes, consisting of glomerules subtended by stipulelike bracts; glomerules with a thick, often dichotomously branched peduncule, up to 3 mm, 4(to 8)-flowered; bracts caducous, (1–)2 × ca. 0.25 mm, puberulous on both surfaces with brownish caducous trichomes; flowers shortly pedicellate, pedicels ca. 1 mm, pubescent with brown trichomes. Hypanthium cupulate; sepals ca. 3 × 1 mm, pale yellow to brown, outer surface pubescent, inner glabrous; petals ca. 1 × 0.5 mm, pale yellow; stamens completely included in the petal blades, with a pale yellow filament and a pale yellow, globose anther ca. 0.2 × 0.2 mm; disc flat, ca. 5 mm diam.; lobes ca. 2 mm, acute, 2/3 as long as the sepals; stigma with 3 short linear lobes, style ca. 0.5 mm. Fruits 0 to 2

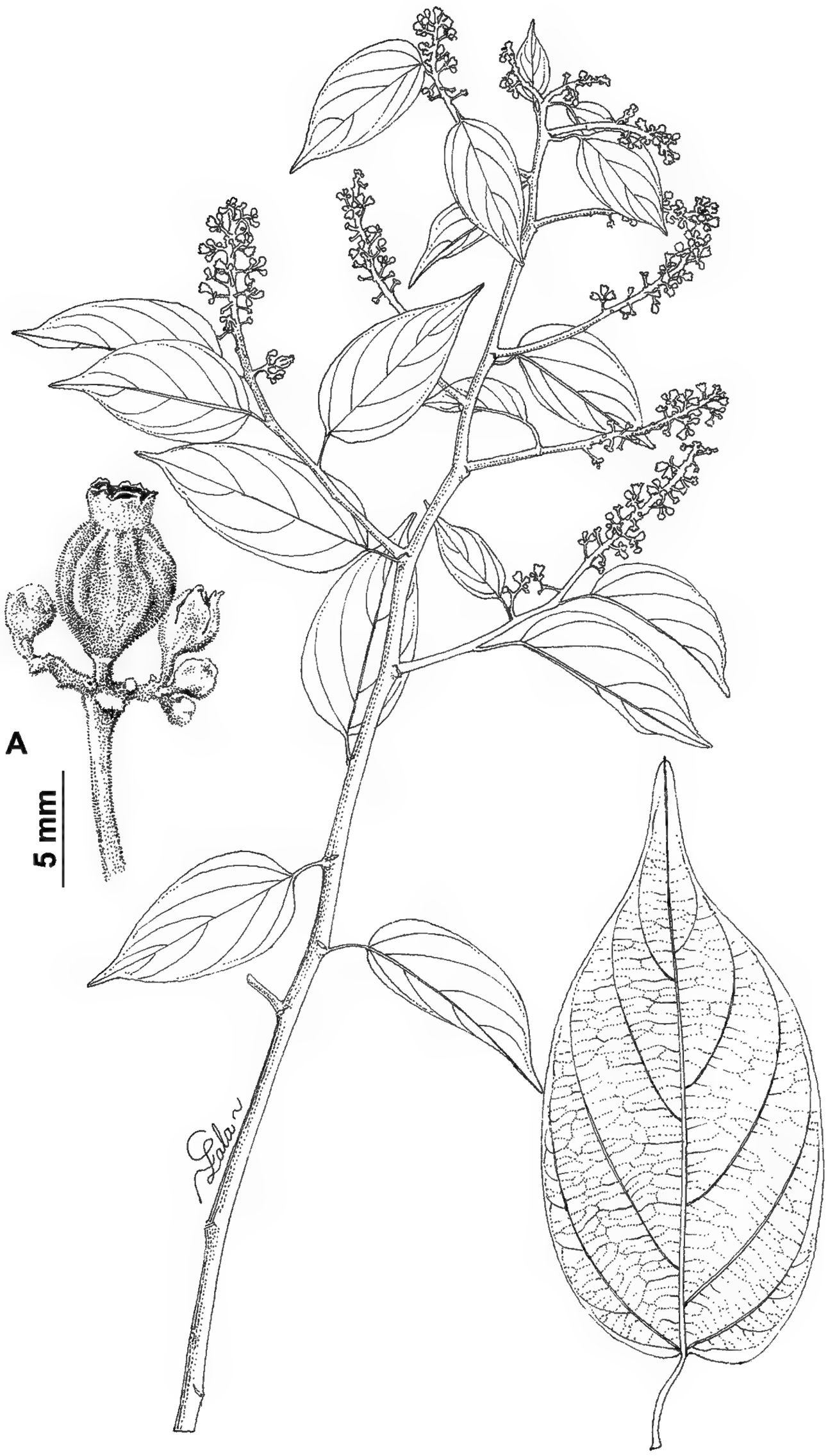


Figure 7. *Gouania gautieri*. —A. Immature fruits. —B. Habit. —C. Elliptic, glabrous leaf. —D. Flower, showing its cupulate form and the lobes of the disc reaching two thirds the length of the sepals. —E. Fruit, showing hirsute indumentum. —F. Seed. A–D drawn from *Rabenantoandro et al. 197* (P); E, F from *Gautier & Chatelain 2647* (TAN).

developing on each glomerule, oblong, large (ca. 1.5 × 1 cm), with a pale brown indument, equally distributed throughout the infructescence; valves ca. 15 × 3 mm; immature fruits globose, with a pale brown indument; seeds pale brown, ovoid, emarginate at apex, hardly flattened, recurved with a line on the inner surface, ca. 7 × 4 × 0.5 mm.

Distribution and ecology. *Gouania gautieri* is endemic to the Manongarivo massif, northwestern Madagascar (Fig. 2C), at an elevational range of 350–1300 m. This species seems to be restricted to degraded forest.

IUCN Red List category. With an EOO of less than 227 km², an AOO of 27 km², and two subpopulations, one of which occurs within a protected area (Manongarivo PA), *Gouania gautieri* is assigned a preliminary status of Endangered (EN

B1ab[ii]; B2ab[ii]) according to IUCN Red List criteria (IUCN, 2001).

Phenology. *Gouania gautieri* is known in flower from September to March, and in fruit at the beginning of April.

Etymology. The new species is named in honor of Laurent Gautier (1960–), Swiss botanist, who has greatly contributed to the knowledge of the flora of the Manongarivo massif and who collected the type specimen.

Discussion. *Gouania gautieri* resembles *G. cupuliflora* in having a cupulate hypanthium and the lobes of the disc two thirds as long as the sepals, but differs most notably in having elliptic to ovate, membranous, glabrous leaves (vs. ovate, subcoriaceous, pubescent with ferruginous trichomes in *G. cupuliflora*); a congested inflorescence (vs. lax); glomerules often with dichotomously branched peduncles (vs. unbranched peduncles); and hirsute pale brown indument on the fruits (vs. pubescent to puberulent with a darker brown indument).

Paratypes. MADAGASCAR. **Antsiranana:** Fiv. Ambanja, Fir. Ambodimanga-Ramena, 13°48′49″S, 48°47′22″E, *J. Rabenantoandro, C. Birkinshaw, B. Razafindrazaka, P. Antilahimena & F. Adamainty 197* (G, K, P, MO); Besinkara, au-dessous d'Ambalafary, 14°04′S, 48°17′E, *L. Gautier & C. Chatelain 2647* (G, K, P, TAN); Manongarivo PA, Antsatroto, 14°05′S, 48°23′E, *S. Malcomber, P. J. Rakotomalaza & J. Raharilala 2287* (MO).

7. Gouania humbertii H. Perrier, Notul. Syst. (Paris) 11: 29. 1943. TYPE: Madagascar. Antsiranana: collines et plateaux calcaires de l'Analamerana, 50–400 m, Jan. 1938 (fl.), *H. Humbert 19233* (holotype, P!; isotypes, G!, TAN!).

Woody liana; stems dark green, drying blackish, glabrous, rather spindly; stipules glabrous, 2.5(–3) × ca. 1 mm; tendrils puberulent with caducous ferruginous trichomes. Leaves orbicular, often conduplicate; petioles to 12 mm, glabrous at maturity; leaf blades (2.5–)3(–3.5) × (2–)3(–3.5) cm; secondary veins alternate, 4 to 5 pairs, not reaching the margin but following it; conspicuous tertiary veins absent, reticulation scalariform; abaxial surface glabrous; midrib and secondary veins slightly prominent; adaxial surface glabrous; margin entire, slightly recurved; base rounded; apex acute. Inflorescences congested, puberulent, spindly, (2.5–)3(–4.5) cm, consisting of glomerules subtended by stipulelike bracts; glomerules shortly pedunculate, to 1 mm, 3(to 5)-flowered; bracts small, glabrous on both surfaces, (0.5–)1 × ca. 0.2 mm; flowers pedicellate up to 1 mm, glabrous at maturity. Hypanthium cupulate; sepals ca. 1.5 × 0.75 mm, pale brown, outer surface puberulent, inner glabrous; petals ca. 1 × 0.2 mm, pale yellow to brown; stamens slightly longer than the petal blades, with a pale yellow filament and a pale yellow, globose anther ca. 0.2 × 0.2 mm; disc flat, ca. 2 mm diam.; lobes ca. 1.25 mm, rounded, generally 3/4 or as long as the sepals; stigma with 3 linear lobes, ca. 0.2 mm; style ca. 0.2 mm. Fruits not known.

Distribution and ecology. *Gouania humbertii* is endemic to the semi-deciduous to decidous forests of northern Madagascar. It has not been recollected at the type locality, Analamerana PA (formerly known as Analamera), but was recently discovered at Daraina (about 50 km to the southeast) (Fig. 2D). The taxon grows on limestone or granitic rocks at an elevational range of 50–400 m.

IUCN Red List category. With only two collections and an AOO of 18 km², *Gouania humbertii* is regarded as Endangered (EN B2ab[ii]), according to IUCN Red List criteria (IUCN, 2001).

Phenology. This species has been collected in flower during January.

Discussion. *Gouania humbertii* shares a lack of conspicuous tertiary veins with *G. lineata* and a cupulate hypanthium with *G. cupuliflora* and *G. gautieri*. Nevertheless, this species can be distinguished from these two and all other Malagasy species by its orbicular, often conduplicate, glabrous leaves and the lobes of the disc reaching three fourths or as long as the sepals. *Gouania humbertii* is the only species known from semi-deciduous to deciduous forests of the Plateau d'Analamerana and is unlikely to be confused with other species occurring in the Daraina forests.

Additional specimen examined. MADAGASCAR. **Antsiranana:** Daraina, partie sud de la forêt de Bekaraoka, 13°11′S, 49°42′E, *Nusbaumer 2050* (G).

8. Gouania laxiflora Tul., Ann. Sci. Nat., Bot. sér. 4, 8: 130. 1857, as "*Guania.*" TYPE: Madagascar. Antsiranana: Ling-Vatou, s.d. (fr.), *A. Bernier 207* (lectotype, designated here, P!). Figure 8A, B.

Gouania comorensis Engl., Veg. Erde 9: 315. 1921, nom. nud., in obs.

Gouania glandulosa Boivin ex Tul. var. *longiloba* H. Perrier, Notul. Syst. (Paris) 11: 31. 1943, nom. nud.

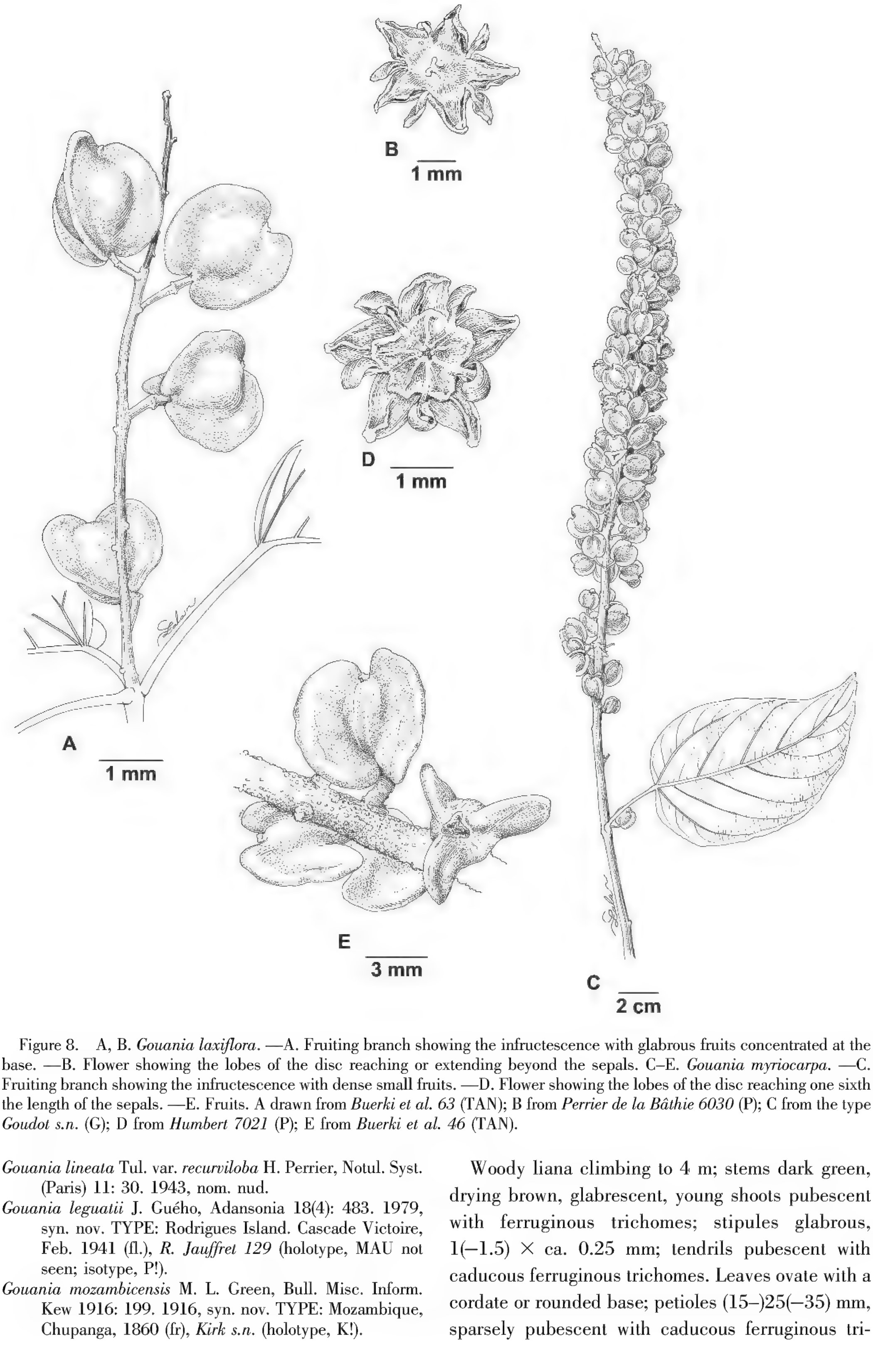


Figure 8. A, B. *Gouania laxiflora*. —A. Fruiting branch showing the infructescence with glabrous fruits concentrated at the base. —B. Flower showing the lobes of the disc reaching or extending beyond the sepals. C–E. *Gouania myriocarpa*. —C. Fruiting branch showing the infructescence with dense small fruits. —D. Flower showing the lobes of the disc reaching one sixth the length of the sepals. —E. Fruits. A drawn from *Buerki et al. 63* (TAN); B from *Perrier de la Bâthie 6030* (P); C from the type *Goudot s.n.* (G); D from *Humbert 7021* (P); E from *Buerki et al. 46* (TAN).

Gouania lineata Tul. var. *recurviloba* H. Perrier, Notul. Syst. (Paris) 11: 30. 1943, nom. nud.

Gouania leguatii J. Guého, Adansonia 18(4): 483. 1979, syn. nov. TYPE: Rodrigues Island. Cascade Victoire, Feb. 1941 (fl.), *R. Jauffret 129* (holotype, MAU not seen; isotype, P!).

Gouania mozambicensis M. L. Green, Bull. Misc. Inform. Kew 1916: 199. 1916, syn. nov. TYPE: Mozambique, Chupanga, 1860 (fr), *Kirk s.n.* (holotype, K!).

Woody liana climbing to 4 m; stems dark green, drying brown, glabrescent, young shoots pubescent with ferruginous trichomes; stipules glabrous, 1(–1.5) × ca. 0.25 mm; tendrils pubescent with caducous ferruginous trichomes. Leaves ovate with a cordate or rounded base; petioles (15–)25(–35) mm, sparsely pubescent with caducous ferruginous tri-

chomes; leaf blades (4.5–)6(–7.5) × (3–)4.5(–5.5) cm; secondary veins alternate, 5 to 8 pairs, not reaching the margin but following it; tertiary veins apparent, arising near the base of the lowest secondary veins, reticulation scalariform; abaxial surface glabrescent, veins puberulous with brown trichomes; midrib, secondary veins, and tertiary veins prominent; adaxial surface glabrous; margin entire to slightly denticulate; base cordate or sometimes rounded; apex acute. Inflorescences spindly, lax, puberulous with pale brown trichomes, (5.5–)10–13(–15) cm, consisting of glomerules subtended by stipulelike bracts, proximal hermaphrodite flowers developing before the distal male flowers; glomerules pedunculate, puberulent with caducous, pale brown trichomes, accrescent, (1–)3 mm, 3- to 5-flowered; bracts small, glabrous on both surfaces, caducous, (0.5–)0.8 × ca. 0.2 mm; flowers pedicellate, pedicels accrescent, (1–)3.5 mm, puberulent with caducous, pale brown trichomes. Hypanthium obconic, becoming subglobose as the capsule develops; sepals ca. 2 × 0.75 mm, pale yellow to brown, outer surface puberulent, inner glabrous; petals ca. 1 × 0.5 mm, white; stamens slightly longer than the petal blades, with a pale yellow filament and a pale yellow, globose anther ca. 0.2 × 0.2 mm; disc flat, ca. 4 mm diam.; lobes 2–2.2 mm, rounded, generally longer or as long as the sepals; stigma with 3 linear lobes, those ca. 0.2 mm, style ca. 2 mm. Fruits 0 to 2 developing on each glomerule, spheroid (ca. 1.5 × 1.5 cm), glabrous, concentrated in the basal part of the infructescence; valves ca. 15 × 4 mm; immature fruits pyriform, glabrous; seeds brown, shiny, and slightly flattened on the inner surfaces, ca. 4 × 3 × 1 mm.

Distribution and ecology. *Gouania laxiflora* is found in mainland Africa (Mozambique and Tanzania) (Drummond, 1966; Johnston, 1972: under *G. scandens*, see discussion below), the Mascarenes (Rodrigues Island), the Seychelles (Aldabra, Île Picard, Cosmoledo), the Comoro Islands (Mayotte), and western Madagascar (Fig. 2D). The species grows in semi-deciduous, deciduous, gallery, and secondary forests, generally on limestone, but sometimes on sand and gneiss at an elevational range from sea level to 350 m.

IUCN Red List category. Within Madagascar, *Gouania laxiflora* has an EOO of 430,841 km², an AOO of 360 km², and 33 subpopulations, 13 of which occur within protected areas (Andohahela, Ankarana, Bemaraha, Beza Mahafaly, Namoroka, Tampoketsa d'Analamaitso, Zombitsy). It is thus assigned a preliminary status of Least Concern (LC) in Madagascar, according to IUCN Red List criteria (IUCN, 2001). We have not assessed its conservation status for other countries within its range.

Phenology. This species has been collected in flower from November to March and in fruit in March and May.

Discussion. Tulasne (1857) designated two syntypes of *Gouania laxiflora*, *Boivin 3366* and *Bernier 207*. The sheet labeled *Boivin 3366* at P is a collection of this species, while sheets with the same collection number at G and K bear material of *G. aphrodes*. To avoid possible confusion, we have lectotypified this species on *Bernier 207*, even though material of this collection is only known to be present at P.

After careful study, we are convinced that this plant is conspecific with *Gouania leguatii* described from Rodrigues Island (Guého, 1997). Material referred to this species has similar cordate leaves, pubescent with caducous ferruginous trichomes, the disc lobes generally as long as or longer than the sepals, and the fruits glabrous and generally concentrated in the basal part of the infructescence. The same is true for the specimens cited in *Flora Zambesiaca* (Drummond, 1966) and in *Flora of Tropical East Africa* (Johnston, 1972) under *G. scandens* from the African mainland (see also discussion under *G. scandens*). *Gouania longipetala* Hemsl. was described for an African species, based on two syntypes from Equatorial Guinea or Gabon (*Mann 17* from Bioko Island "Fernando Po" and *Mann 1813* from Muni River "Kongui River") and one, *Kirk s.n.*, from Chupanga, Mozambique (Hemsley, 1868). Green (1916) realized that this material represents two different species and described *G. mozambicensis* to accommodate the East African entity based on the Kirk specimen, while retaining the name *G. longipetala* for the Central African species. Later Hallé (1962) designated *Mann 17* from Bioko as the "Type," thus effecting lectotypification of *G. longipetala*. Kirk's specimen from Mozambique is a specimen of *G. laxiflora*, and we include *G. mozambicensis* in the synonymy of this species. *Gouania laxiflora* is the only species shared between mainland Africa and Madagascar.

Gouania laxiflora differs from *G. perrieri*, to which it is most similar, by its slightly denticulate leaf margin (vs. shallowly crenate margin in *G. perrieri*), lobes of the disc as long as or longer than the sepals (vs. lobes of the disc reaching one fourth of the sepals), and its immature pyriform fruits (vs. immature fruits winged).

Additional specimens examined. COMORO ISLANDS. s. loc., fl. & imm. fr., *Boivin s.n.* (K). **Mayotte:** Grande Terre, Mtsamboro, Ilot Mtsamboro, *Barthelat et al. 198* (P); Grande Terre, Mamoudzou, Ilt Bouzi, *Barthelat et al. 355* (G, K, MO, P); Boeni, *Boivin 3366* (P); Coconi, *Lorence 2818* (MO); Chissioi Caroni (islet off SW coast), *Lorence & Roulleau 2814* (MO); Dapani, *Pascal 568* (P); Chissious Mtsamboro, près du sommet, *Pignal & Pibot 1183* (K, P); Baie de Langoni, *Tinguy 1019* (P). MADAGASCAR. s. loc., "Central Madagascar," fl., *Baron 3532* (K), fl., *Baron 4815* (K), fr., *Baron 4819* (K, P); fl., *Baron 4823* (K); fl., *Grevé 107* (G, P). **Antsiranana:** Ankarana PA, campement des anglais, *Andrianantoanina et al. 841* (P); Ankarana PA, Matsaborimanga, piste Grim, *Bardot-Vaucaulon et al. 1170* (K, MO, P, TAN); Ankarana PA, *Bardot-Vaucaulon 1549* (K, MO, P, TAN); Daraina, Forêt de Bekaraoka, *Gautier et al. 4368* (G); Collines et Plateaux calcaires de l'Ankarana, *Humbert 18822* (P), *Humbert 18907* (G, P, TAN), *Humbert 32437* (P); Ankarana PA, near Campement des Anglais, *Leuwenberg et al. 14329* (K, MO, P, TAN, WAG); Montagne d'Ambre, versants ouest, *Gautier et al. 5251* (G, K, MO, P, TEF); Montagne d'Ambre, *Razanajatovo et al. 30* (G, K, MO, P, TEF); Montagne des Français, *Perrier de la Bâthie 17523* (P); Ankarana PA, *Randriambololona et al. 36* (P). **Fianarantsoa:** Rte. Ihosy-Ivohibe, Km 40, *Peltier & Peltier 5585* (P). **Mahajanga:** Sakoany, *Callmander & Phillipson 697* (G, K, MO, P, TAN, US, WAG); Forêt d'Ambanjabe, *Cours 3951* (P, TAN); Plateau d'Ankaro, *Descoings 3368* (TAN); Morondava, *Grevé s.n. comm. Dr Baillon* (K); Forêt d'Ambanjabe, Mont Marovoay, *Herb. Inst. Sci. Madag. 3951* (TAN); Rte. d'Ambato-Boeni, *Jacquemin 912* (P); Forêt d'Analamaitso, *Keraudren 1703* (P); Bemaraha PA, *Leandri 576* (P); Bemaraha PA, *Leandri 580* (P), *Leandri 863* (P), *Leandri 932* (MO, P), *Leandri 940* (P), *Leandri 968* (P), *Leandri s.n.* (P); Vers Ambodiriana, *Leandri 2704* (P); Rte. de Majunga, P.K. 538, *Morat 2719* (P, TAN); Namoroka PA, *Morat 4809* (P, TAN); Amdriba (RN27), *Peltier & Peltier 5755* (P); Bois le long du Jabohazo, Antririhitra près de Mont Tsitondraina, *Perrier de la Bâthie 1590* (K, P); Marofotra, rive gauche de l'Ikopa en face de Maevatanana, *Perrier de la Bâthie 6027* (P), *Perrier de la Bâthie 6029* (P); Mariarana près du Mont Tsitondroina (Boina), *Perrier de la Bâthie 6028* (P); environs d'Amboina près de Majunga, *Perrier de la Bâthie 6030* (P); en chemin de Maevatanana, *Perrier de la Bâthie 6039* (P); Boina, *Perrier de la Bâthie 14647* (P); Antsalova, *Réserves Naturelles 11107* (P); Soalala, *Réserves Naturelles 2138* (P, TAN); Namoroka PA, *Service Forestier 11-SF* (P); environs de Berivotra, *Service Forestier (Capuron) 162* (P); Antsalova, *Service Forestier 19840* (TEF); Berano, *Service Forestier 26518* (P, TEF); Amboina, *Sol 34* (P); 14 km E of Antsalova, *Villiers et al. 4777* (K); 12 km ESE Ankiliromotsy, 26 km SE Antsalova, *Villiers et al. 4997* (K, P). **Toliara:** Manasoa Mahafaly, *Afzelius s.n.* (MO, P); S of Andranovory, betw. Ambatry & Toboky Mitsy, *Anderberg, Smedmark, Axelius, Manns & Englund 166* (P, S); [25 km NE of] Andranovory, *Andriamahay et al. 560* (K); Mahabo, *Andriamahay et al. 820* (P); Befandiana-Sud, *Appert 68* (K, WAG); Ankilizato (Mont Mahabo), *Bosser 4611* (TAN); après Mahaboboka en allant à Toliara, *Buerki et al. 63* (K, MO, P, TAN); 23–43 km E of Tulear along rd. to Andranovory, *Croat 31059* (K, MO); Rte. Nationale 10 betw. Tongobory & Betioky, *Croat 31232* (MO); RN10 betw. Ejeda & Ampanihy, betw. PK 200 & 250, *Croat 31339* (MO, TAN); 1–4 km W of Etrobecke, *Croat 31448* (MO, TAN); along Rte. 13 from Ambovombe to Antanimora, *Croat 32015* (MO, TAN); Ambovombe (Mont Angavo), *Decary 8610* (P); ferme de Mahabo, *Dequaire 27034* (P, TAN); Sud Ambovombe, *Descoings 1464* (MO, TAN); Manombo, *Douliot s.n.* (P); 12 km SW of Ampanihy on rte. to Androka, *Du Puy & Du Puy MB579* (TAN); Mahafaly plateau, ca. 7 km S of Beahitse on RN10, *Du Puy et al. MB36* (TAN); ca. 17 km N of Ejeda on Rte. Nationale 10, *Du Puy et al. MB608* (TAN); Fiherenena, *Geay 3345* (P); Morondava, *Grevé 111* (K, P, TAN); Gorges du Fiherenana entre Beantsy et Anjamala, *Humbert 19909* (P); de la vallée de la Sakamena à la vallée de la Sakoa (bassin de l'Onilahy), *Humbert 29409* (P); RN7 at 98 km NE of Tulear, 400 m, *Lorence 1920* (TAN); Rte. Ankazoabo, *Morat 2908* (TAN); Piste Ankazoabo après le village de Laborano, *Morat 3580* (P, TAN); 55 km NE of Morondava via rte. 8, Kirindy Forest, *Noyes et al. 1052* (P, WAG); Beza Mahafaly PA, parcelle 1, *Phillipson 1687* (K, MO, P, TAN); 64 km along RN55 from Morombe, Mangoky valley, *Phillipson et al. 4140* (P); Analamaiky, *Rakotondranony et al. 212* (K); Ranobe Forest, *Phillipson et al. 5880* (G, K, MO, P, TAN, WAG); Andohahela PA, parcelle 3, *Randriamampionona 272* (P, WAG); Andohahela PA, parcelle I, *Randriamampionona 808* (P). MASCARENE ISLANDS. **Rodrigues Island:** *Balfour s.n.* (K, P), *Jauffret 105* (P); Cascade Momoac, *Lesouef s.n.* (P). (African specimens examined are not listed). SEYCHELLES. **Aldabra. West Island (Île Picard):** back of settlement, 2–3 m, *Fosberg 48699* (K, MO), *Fosberg 48806* (MO), *Fosberg 48831* (K, MO), *Fosberg 49499* (MO); coast N of settlement just S of Anse Var, *Fosberg 49484* (K); settlement, *Renvoize 715* (K); near settlement, *Stoddart 967* (K); 50 m E of laboratory, *Wood 1610* (K); no precise locality, *Abbott s.n.* (K), *Dupont 12* (K), *Dupont 129* (K), *Fryer 76* (K), *Renvoize 1362* (K), *Thomasset 231* (K). **Cosmoledo:** *Thomasset s.n.* (K).

9. Gouania lineata Tul., Ann. Sci. Nat., Bot. sér. 4, 8: 131–132. 1857, as "*Guania.*" TYPE: Madagascar. Antsiranana: Nosy Be, Lokobe, ("Nossibé, Forêt de Loucoubé"), [13°25′S, 48°19′E], Dec. 1850 (fr.), *L. H. Boivin 2171/2b* (lectotype, designated here, P 00386419!; isotype, P 00386420!). Figure 6A–C.

Woody liana climbing to 4 m; stems green, drying dark brown, glabrescent, young shoots puberulous with pale trichomes; stipules glabrous, 2(–3) × ca. 0.75 mm; tendrils puberulous. Leaves ovate to elliptic; petioles (5–)10–15(–20) mm, glabrous; leaf blades (4–)5.5(–12) × (2–)3.5(–6) cm; secondary veins alternate, 6 to 7 pairs, not reaching the margin but following it; conspicuous tertiary veins absent, reticulation scalariform; abaxial surface glabrous, veins puberulous with pale trichomes; midrib and secondary veins prominent; adaxial surface glabrous; margin entire, slightly recurved; base rounded; apex acute. Inflorescences congested, pubescent with a white indument, (5.5–)8.5(–12) cm, consisting of glomerules subtended by stipulelike bracts; glomerules sessile, sometimes shortly pedunculate at the base of the inflorescence, 2(to 5)-flowered; bracts

pubescent with pale trichomes on the outer surface, glabrous on the inner surface, caducous, (1.5–)2 × ca. 0.5 mm; flowers pedicellate, pedicels accrescent, (1–)2.5 mm, pubescent with whitish trichomes. Hypanthium obconic, becoming subglobose as the capsule develops; sepals ca. 1.5 × 0.5 mm, pale yellow, outer surface pubescent, inner glabrous; petals ca. 1 × 0.5 mm, pale yellow; stamens slightly longer than the petal blades, with a pale yellow filament and a pale yellow, globose anther ca. 0.2 × 0.2 mm; disc flat, ca. 3 mm diam., pale yellow to white; lobes ca. 0.5 mm, acute to slightly truncate, 1/3 as long as the sepals; stigma with 3 linear lobes, those ca. 15 mm; style ca. 2 mm. Fruits 1 to 2 developing on each glomerule, small, oblong (ca. 0.5 × 1 cm), glabrous, densely arranged throughout the infructescence; valves ca. 5 × 5 mm; immature fruits globose, puberulous with whitish trichomes; seeds brown, shiny, ovoid to pyriform and slightly flattened, ca. 3 × 2 × 0.5 mm.

Distribution and ecology. *Gouania lineata* occurs in western and northern Madagascar (Fig. 2B) in evergreen, semi-deciduous forests and secondary vegetation on sand or limestone at an elevational range from sea level to 900 m.

IUCN Red List category. Based on an EOO of 309,667 km², an AOO of 207 km², and 21 subpopulations, eight of which occur within protected areas (Ankarafantsika, Isalo, Manongarivo, Namoroka, Tsaratanana, Zombitsy), we assign *Gouania lineata* a preliminary status of Least Concern (LC), according to IUCN Red List criteria (IUCN, 2001).

Phenology. *Gouania lineata* is known in flower from January to May and in fruit from June to January.

Discussion. *Gouania lineata* is based on multiple syntypes with specimens only known to be present at P. One of these collections, *Pervillé 617*, is represented by two sheets, and the other, *Boivin 2171/2*, is represented by three sheets. The Pervillé collection from "Ambongo" is dated 15 February 1841 and clearly represents a single gathering, both sheets bearing specimens with similar very young inflorescences with no open flowers or fruits. The three Boivin sheets represent two separate gatherings, presumably put together later under a single number (possibly explaining the dual number "2171/2" that appears on each of the sheets, but see the note below about *Boivin 2171*). The first of the sheets (P 00386418) bears a flowering specimen and an original label with the information: "Nossi-Cumba. juill. 1850. fr. / Nossibé, Forêt de Loucoubé, mars 1851. fl.," together with a Paris Herbarium label with the printed information "Madagascar, Voyage de M. Boivin, 1847–1852," on which the name *G. lineata*, the reference to the Tulasne (1857) publication, and the collection number are handwritten. The other two sheets of *Boivin 2171/2* each bear similar Paris Herbarium labels bearing exactly the same printed and handwritten information as the first sheet, but lack original labels with the collection locality or date. One of these sheets (P 00386418) bears a specimen with mature fruits and old infrutescences; the second (P 00386420) bears a specimen that is almost sterile, bearing no fruits and just a few flowers on a highly reduced inflorescence. We conclude that these flowering and fruiting specimens correspond to the two gatherings noted on the original label that is present on the first sheet. To distinguish the gatherings, we designate the fruiting collection ("fr.") from Nosy Kumba ("Nossi-Cumba") as *Boivin 2171/2a* and the flowering collection ("fl.") from Lokobe Forest on Nosy Be ("Nossibé, Forêt de Loucoubé") as *Boivin 2171/2b*. We select the better of the two Nosy Be specimens, which bears the original label, as the lectotype. It should be noted that Boivin also collected the type specimen of *G. aphrodes* at Nosy Be under the number 2171.

Gouania lineata is morphologically most similar to *G. myriocarpa* Tul.; both species possess small glabrous fruits congested along the entire infructescence. However, *G. lineata* can be distinguished from *G. myriocarpa* by the lack of conspicuous tertiary veins on its leaves and by the lobes of the disc reaching one third of the sepals (vs. lobes of the disc reaching one sixth of the sepals). Furthermore, while *G. lineata* is widespread in western Madagascar, *G. myriocarpa* is confined to the eastern escarpment and the central plateau.

Additional specimens examined. MADAGASCAR. s. loc., fl., *Boivin s.n.* (K); fl., *Service Forestier 9* (P, TAN). **Antananarivo:** forest remnant betw. Ambaranala & Tsiroanomandidy, *Barnett et al. 399* (K, P, TAN); Rebord occidental Bongolava, O Tsiroanomandidy, *Morat 4597* (P, TAN). **Antsiranana:** Mandrizavona, Antsahafaly River, *Antilahimena 419* (G, MO, P, TAN); Nosy Kumba ("Nosi-Cumba"), *Boivin 2171/2a* (P); Andranosavony, *Buerki & Wohlhauser 34* (K, MO, P, TEF); Besinkara, *Gautier et al. 2401* (G, K, TAN); Saharenana, Sadjoavato, Forêt de Sahafary, *Hongwa et al. 205* (Centre National d'Application de Recherche Pharmaceutique [CNARP], MO, P); Ambilobe, Ambakirano, Behefaka, Anjahana, forêt de Belifilelatra, *Hongwa et al. 309* (CNARP, MO, P, TAN); Ambilobe, Forêt Ambohibe, *Leopold et al. 120* (MO, P, TAN); Massif du Manongarivo, *Perrier de la Bâthie 1552* (P), *Perrier de la Bâthie 6042* (P); Daraina, Forêt d'Antsahabe-nord, *Ranirison 767* (G, MO); Bemanevoka, Ambobaka, *Ratovoson et al. 193* (G, MO, P, TAN); Ambodisakoana, *Totozafy Be 552* (G, P). **Fianarantsoa:** Isalo, *Homolle 1462* (P); environs

d'Ihosy, *Humbert 14464* (P); Ihosy, *Peltier & Peltier 4887* (P). **Mahajanga:** Antsianitia, *Callmander & Phillipson 677* (G, K, MO, P, TAN, US); Namoroka PA, *Decary 18981* (P); vic. of Lac Ampijoroa, *Gentry 11471* (K, P, TAN); Bongolava de Port Bergé, *Morat 4454* (P, TAN); Boina, *Perrier de la Bâthie 6037* (P); Ankarafantsika PA, *Perrier de la Bâthie 14694* (K, P, TAN); Vallon de Mangotroky, près Soalala (Ambongo), *Perrier de la Bâthie 1552 bis* (P); Ambongo, *Pervillé 617* (P); Namoroka PA, *Réserves Naturelles 8648* (P, TEF); Lac Ampijoroa, *Service Forestier (Rabevohitra) 29773* (TEF). **Toliara:** Zombitsy PA, *Allorge 2110* (P); Zombitsy PA, *Croat 30720* (MO, TAN); E of Tulear betw. 45 & 55 km E of Tulear on rd. to Andranovory, *Croat 31070* (MO, TAN); Plateau gréseux à l'Est de la vallée Sikily au NW d'Ankazoabo, *Humbert 29725* (P); Forêt de Marosalaza, *Petter 30, 32* (P); Zombitsy PA, *Randrianaivo et al. 305* (P).

10. Gouania mauritiana Lam., Encycl. 3: 5. 1789. TYPE: Mauritius (cultivated). Cultivée au Jardin du Roi, s.d. (st.), *Herbier Lamarck s.n.* (lectotype, designated here, P-LA!). EPITYPE: Réunion. Mare sèche, Cilaos, 24 Jan. 1983, *T. Cadet 6500* (epitype, P 00386378!).

Gouania incisa Vahl, Symb. Bot. (Vahl) 3: 101. 1794, nom. superfl.

Gouania sericea Hils. ex C. Presl, Abh. Königl. Böhm. Ges. Wiss., ser. 5 39, 1844, nom. superfl.

Gouania sericea Sieber ex Tul., Ann. Sci. Nat., Bot. sér. 4, 8: 134. 1857, nom. inval. (ICBN, Art. 34.1a).

Woody liana; stems dark green, drying brown to ferruginous, densely lanate with ferruginous trichomes; stipules pubescent with a ferruginous indument on the upper surface and glabrous on the inner surface, (4–)5(–6) × ca. 3 mm; tendrils pubescent. Leaves lanceolate to deltoid; petioles (8–)10(–15) mm, densely pubescent with a ferruginous trichome; blade (3.5–)4.5–5(–6) × (2.5–)3.5(–4) cm; secondary veins alternate, (5 to)6(to 7) pairs, reaching and following the margin; tertiary veins apparent, 5(to 7) pairs, arising near the base of the lowest secondary veins, fine reticulation obscure; abaxial surface lanate with whitish trichomes on the limb, and ferruginous trichomes on the midrib, secondary veins, and tertiary veins; adaxial surface pubescent with appressed whitish trichomes; margin serrate; base rounded to shallowly cordate; apex acuminate. Inflorescences ± lax, densely pubescent with a reddish indument, (5.5–)6–7(–8) cm, consisting of compact glomerules subtended by stipulelike bracts; glomerules sessile, up to 15-flowered, glomerules at the base of the inflorescence; bracts triangular-lancelolate, densely pubescent with reddish trichomes on the outer surface and glabrous on the inner, ± persistent, (5–)6 × ca. 2 mm; flowers shortly pedicellate, pedicels ca. 1.5 mm, covered by a whitish indument. Hypanthium obconic, becoming subglobose as the capsule develops; sepals ca. 1.5 × 2 mm, pale yellow, outer surface densely pubescent with whitish trichomes at the base and reddish trichomes at the apex, inner glabrous; petals ca. 1 × 0.25 mm, whitish; stamens partially included in the petal blades, with a pale yellow filament and a pale yellow, globose anther ca. 0.2 × 0.2 mm; disc flat, ca. 2.5 mm diam.; lobes ca. 0.4 mm, slightly emarginate, 1/4 as long as the sepals; stigma with 3 linear lobes, those ca. 0.75 mm, style ca. 1 mm. Fruits 1 developing on each glomerule, oblong (ca. 1 × 1.2 cm), glabrous, densely arranged; valves ca. 10 × 5 mm; immature fruits globose, with a whitish indument, becoming reddish when mature; seeds pale brown, ovoid and slightly flattened, ca. 3.5 × 2 × 0.5 mm.

Distribution and ecology. Endemic to Réunion Island, *Gouania mauritiana* is found in humid, evergreen montane rainforest and secondary vegetation at an elevational range of ca. 1000 m.

IUCN Red List category. *Gouania mauritiana* has only been collected at one locality (Cilaos) on Réunion Island in the past 100 years, and only one older collection can be accurately georeferenced. Neither locality is in a protected area, so with an AOO of 18 km² the species is regarded as Endangered (EN B2ab[ii]), according to IUCN Red List criteria (IUCN, 2001).

Phenology. This species has only been collected in fertile condition (flower and fruit) in January.

Discussion. *Gouania mauritiana* was described by Lamarck based on a plant cultivated in the Jardin du Roi in Mauritius. However, when he chose the epithet he had not seen specimens from Réunion Island where the species is native, and he was apparently unaware that the plant did not originate from Mauritius. Although there can be no doubt about the identity of the type specimen, it is sterile; we, therefore, select a modern specimen, *Cadet 6500*, which bears both flowers and fruit, to serve as an interpretative epitype.

In this treatment we adopt a much narrower concept of *Gouania mauritiana* than Perrier de la Bâthie (1943, 1950). Herein we limit *G. mauritiana* to the typical subspecies and recognize the three other subspecies (*G. mauritiana* subsp. *aphrodes*, *G. mauritiana* subsp. *myriocarpa*, and *G. mauritiana* subsp. *pannigera*) at the rank of species, as established by Tulasne in 1857. *Gouania mauritiana* differs from these species by its lanceolate to deltoid leaves (vs. ovate in the other three), the abaxial surface covered by woolly whitish trichomes (vs. a beige indument in *G. aphrodes*, but glabrescent in *G. myriocarpa*, and whitish or grayish indument in *G.*

pannigera), its disc lobes reaching one fourth of the length of the sepals (vs. lobes of the disc reaching one sixth of the sepals in *G. aphrodes*, *G. myriocarpa*, and *G. pannigera*). Furthermore, *G. mauritiana* appears to be endemic to Réunion Island, whereas *G. aphrodes* occurs in Madagascar and the Comoro Islands, and *G. pannigera* and *G. myriocarpa* are endemic to Madagascar.

Additional specimens examined. RÉUNION ISLAND. s. loc., *Barclay s.n.* (K); fl. & imm. fr., *Boivin 1383* (P); fl., *Boivin s.n.* (K); fr., *Commerson s.n.* (K, P); fl., *De L'Isle 605* (P); fl., *Du Petit Thouars s.n.* (P); fl., *Herb. Colonial ministère de la marine s.n.* (P); fl., *Hilsenberg s.n.* (K); fl., *Richard s.n.* (P); Crête gauche du Bulon, au-dessus de Dattier, *Boivin 1383/2* (G, K, P); Cilaos, *Cadet 724* (P), *Cadet 1831* (P).

11. Gouania myriocarpa Tul., Ann. Sci. Nat., Bot. sér. 4, 8: 132. 1857, as "*Guania*." *Gouania mauritiana* Lam. subsp. *myriocarpa* (Tul.) H. Perrier, Notul. Syst. (Paris) 11: 33. 1943. TYPE: Madagascar. Toamasina: Ambanivoules, côte orientale, s.d. (fr.), *J. P. Goudot s.n.* (holotype, G!; isotype, G!). Figure 8C–E.

Gouania glandulosa Boivin ex Tul. var. *breviloba* H. Perrier, Notul. Syst. (Paris) 11: 32. 1943, nom. nud.

Woody liana climbing to 10 m; stems dark green, drying dark brown to black, tomentose with rather caducous ferruginous trichomes; stipules glabrous, 3(–4) × ca. 0.75 mm; tendrils pubescent. Leaves ovate; petioles (5–)10–15(–20) mm, pubescent with ferruginous trichomes; leaf blades (4.5–)5.5–6(–7) × (2.5–)3(–4) cm; secondary veins alternate, 4 to 5 pairs, not reaching the margin but following it; tertiary veins conspicuous, arising near the base of the lowest secondary veins, reticulation scalariform; abaxial surface glabrescent, pubescent with ferruginous trichomes on the veins; midrib, secondary veins, and tertiary veins prominent; adaxial surface glabrous; margin shallowly crenulate; base rounded, sometimes shallowly cordate; apex acute. Inflorescences congested, pubescent with hirsute ferruginous trichomes, (8–)12(–25) cm, consisting of glomerules subtended by stipulelike bracts; glomerules sessile or shortly pedunculate, (2 to)4-flowered; bracts scarious, small, glabrous on both surfaces, ± persistent, (1–)2 × ca. 0.5 mm; flowers with a spindly pedicel (1–)1.5(–2) mm, covered by a whitish indument. Hypanthium obconic, becoming subglobose as the capsule develops; sepals ca. 1.5 × 0.5 mm, reddish, outer surface pubescent to glabrous, inner glabrous; petals ca. 0.75 × 0.25 mm, reddish; stamens slightly longer than the petal blades, with a pale red filament and a pale red, globulose anther ca. 0.2 × 0.2 mm; disc flat, ca. 2 mm diam.; lobes ca. 0.25 mm, truncate or slightly emarginate, 1/6 as long as the sepals; stigma with 3 linear lobes, those ca. 0.8 mm; style ca. 1 mm. Fruits 1 or 2 developing on each glomerule, small, spheroid (ca. 0.6 × 0.6 cm), glabrous, densely arranged throughout the infructescence; valves ca. 6 × 4 mm; seeds brown, shiny, ovoid, ca. 2 × 1 × 0.3 mm.

Distribution and ecology. *Gouania myriocarpa* occurs in eastern Madagascar (Fig. 2D) in evergreen montane rainforest and secondary forests on basaltic rocks, gneiss, and laterite soils at an elevational range of (500–)800–100(–1400) m.

IUCN Red List category. With an EOO of 164,280 km², an AOO of 216 km², and 17 subpopulations, seven of which occur within protected areas (Andohahela, Anjanaharibe-Sud, Analamazoatra-Perinet, Marojejy, Masoala, Montagne d'Ambre, Ranomafana), *Gouania myriocarpa* is thus assigned a preliminary status of Least Concern (LC), according to IUCN Red List criteria (IUCN, 2001).

Phenology. This species is known in flower from November to February and in fruit from March to July.

Discussion. Tulasne described *Gouania myriocarpa* together with six other species of *Gouania* in his treatment of the Rhamnaceae for *Florae Madagascariensis* (Tulasne, 1857). Later, adopting broad species concepts, Perrier de la Bâthie (1943) reduced three of these species (*G. aphrodes*, *G. myriocarpa*, and *G. pannigera*) to subspecies of *G. mauritiana*. We agree with Tulasne's narrower delimitation and these taxa are again recognized at the species level.

Furthermore, Perrier de la Bâthie did not examine the type specimen of *Gouania myriocarpa*, citing "Ambanivola, *Goudot* (in Herb. Delessert, *non vu*)" (Perrier de la Bâthie, 1950: 46), and, as a result, he completely misinterpreted this taxon. In his treatments for *G. mauritiana* subsp. *myriocarpa* (Perrier de la Bâthie, 1943: 33; 1950: 46), he included specimens that we now refer to *G. phillipsonii*, which we describe as new below. On the other hand, he referred specimens of true *G. myriocarpa* to his new variety, *G. glandulosa* var. *breviloba* (Perrier de la Bâthie, 1943: 32; 1950: 43), a name that was not validly published.

Gouania myriocarpa is morphologically most similar to *G. lineata*, both having glabrous fruits congested along their entire infructescences (see *G. lineata* for further comparison). *Gouania myriocarpa* can, however, be recognized easily among the Malagasy species by the presence of the ferruginous trichomes on the petioles, along the veins of the abaxial leaf surface, and the inflorescence. The lobes

of its floral disc are one sixth as long as the sepals, and the glabrous fruits are densely arranged on the infructescence.

Additional specimens examined. MADAGASCAR. s. loc., fl., *Baron 239* (K, P). **Antsiranana:** Montagne d'Ambre PA, SE du Lac Texier, *Debray H1341D* (P); Anjanaharibe-Sud PA, *Rasoavimbahoaka & Ravelonarivo 215* (P, TAN); Marojejy PA, *Rasoavimbakoaka 566* (K, P, TAN); Anjanaharibe-Sud PA, *Ravelonarivo & Rasovimbahoaka 74* (P, TAN, WAG); Montagne d'Ambre PA, *Schledl 167* (TAN). **Fianarantsoa:** Iakora, forêt de Sakalava, *Andrianjafy et al. 982* (MO, P, TAN); Ranomafana, bord de la route nationale, *Buerki et al. 46* (BR, G, K, MO, P, TAN, US, WAG); Ambohimotombo, *Forsyth-Major s.n.* (G); haute vallée de la Rienana (bassin du Matitanana), *Humbert 3626* (P, TAN); massif de l'Ivakoany, *Humbert 7021* (P); Ranomafana PA, parcelle 3, *Rakoto 392* (P); Analamanavaona, proche Vohimary, *Rakotovao 652* (P); Andrambovato, *Service Forestier (Capuron) 265* (P, TEF). **Toamasina:** Moramanga, Ambatovy, *Antilahimena et al. 5297* (MO, P, TAN, TEF), *Antilahimena et al. 5375* (MO, P, TAN, TEF), *Antilahimena et al. 6085* (MO, P, TAN, TEF); Andranobe, SO du lac Alaotra, 1100 m, *Bosser 19865* (MO, P, TAN); Ambatoharanana near Antsevabe, *Cours 4050* (P, TAN); Bemainty, vers 850 m, *Cours 4205* (P, TAN); Perinet PA, *Cremers 1492* (P, TAN); along Rte. 2 betw. Perinet & Beforona, *Croat 32330* (K, P, TAN); S de Moramanga, *Decary 6911* (K, P); S de Moramanga, *Decary 7123* (P, TAN); RN2 at 15 km W of Perinet, *Lorence 2013* (P, TAN); Analamazoatra-Perinet PA, 1040 m, *Lowry & Schatz 4304* (K, P, TAN, WAG); Ambohilero, logging rd. from Antserabe, 1120 m, *Lowry et al. 6615* (MO, P, TAN); vic. of 13 km marker on mine rd. to Tsaravoniana encampment, *Noyes et al. 990* (P, WAG); bords de Mangoro entre Beparasy et Moramanga, *Perrier de la Bâthie 17199* (P); Rivière Sahanana, barrière du Sakaleony, *Perrier de la Bâthie 6014* (P); Antananarivo on rd. to Perinet, *Phillipson 1624* (K, P, TAN, WAG); Ambatovy, *Rakotomalaza 1160* (P); Betampona PA, *Réserves Naturelles 3672* (MO, P, TAN); Ambohitralanana, *Réserves Naturelles 8814* (P, TAN); Perinet PA, *Service Forestier 1422-SF* (P, TAN, TEF); Ambodilongotra, Moramanga, *Service Forestier 26772* (P, TEF); 12 km bifurcation entre rte. de Lakanto et Moramanga, *Service Forestier 29722* (TEF). **Toliara:** Vohifeno, *Beaujard 375* (P); montagnes gneissiques entre le col du Kalambatritra et la vallée de la Manambolo, affluent de l'Ionaivo, *Humbert 12099* (P); Andohahela PA, Euanihilia, *Réserves Naturelles 5157* (P).

12. Gouania pannigera Tul., Ann. Sci. Nat., Bot. sér. 4, 8: 134. 1857, as "*Guania*." *Gouania mauritiana* Lam. subsp. *pannigera* (Tul.) H. Perrier, Notul. Syst. (Paris) 11: 33. 1943. TYPE: Madagascar. Antananarivo: bois aux environs de Tananarive, s.d. (fl. & imm. fr.), *J. P. Goudot s.n.* (holotype, G!; isotype, G[2]!). Figure 9E–H.

Woody liana climbing to 10 m; stems dark green, drying blackish, densely pubescent with a red-brown indument; stipules densely pubescent on the 2 surfaces with reddish brown trichomes, 2(–3) × ca. 1 mm; tendrils pubescent. Leaves ovate, discolorous when dried; petioles (6–)10(–15) mm, pubescent with a reddish brown trichome; leaf blades (3–)4–5(–7) × (2–)3(–3.5) cm, discolorous; secondary veins alternate, sometimes subalternate, 5 to 6 pairs, reaching and following the margin; tertiary veins apparent, 2(to 4) pairs, arising generally from the first pair of secondary veins, sometimes from the second, fine reticulation obscure; abaxial surface lanate with whitish or grayish indument; midrib, secondary veins, and tertiary veins covered by a whitish indument that becomes reddish when dried; adaxial surface pubescent with brown trichomes; margin entire, sometimes with 1 or 2 teeth near the base; base rounded; apex rounded or subacute. Inflorescences congested, densely pubescent with a reddish indument, (4–)7–8(–12) cm; glomerules shortly pedunculate, peduncles up to 1.5 mm, 10-flowered; bracts densely pubescent, persistent, (2–)3 × ca. 1 mm; flowers and fruits shortly pedicellate, pedicels up to 1 mm, covered by a reddish indument. Hypanthium obconic, becoming subglobose as the capsule develops; sepals ca. 2 × 1 mm, pale yellow to whitish, outer surface densely pubescent, inner glabrous; petals ca. 1 × 0.25 mm, whitish; stamens totally included in the petal blades, with a pale yellow filament and a pale yellow, globose anther ca. 0.2 × 0.2 mm; disc flat, ca. 3 mm diam.; lobes ca. 0.3 mm, truncate or somewhat emarginate, 1/6 as long as the sepals; stigma with 3 linear lobes, those ca. 0.75 mm, style ca. 1 mm. Fruits 0 to 1 developing on each glomerule, oblong (ca. 1 × 1.4 cm), sparsely pubescent with reddish trichomes, equally distributed throughout the infructescence, only the distal flower of each glomerule develops to a fruit, the others falling and leaving conspicuous scars; valves ca. 10 × 7 mm; immature fruits globose, with a whitish indument that becomes reddish; seeds pale brown, ovoid and slightly flattened, ca. 4 × 3 × 1 mm.

Distribution and ecology. *Gouania pannigera* is distributed in central Madagascar (Fig. 2B) in evergreen montane rainforest and secondary forest on quartzite, sand, and basalt rocks at an elevational range of 800–1500 m.

IUCN Red List category. With an EOO of 215,709 km², an AOO of 360 km², and 34 subpopulations, six of which occur within five protected areas (Ambohitantely, Andringitra, Isalo, Tsaratanana, Zahamena), *Gouania pannigera* is thus assigned a preliminary status of Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Phenology. This species has been collected in flower from January to April and fruiting at the end of April.

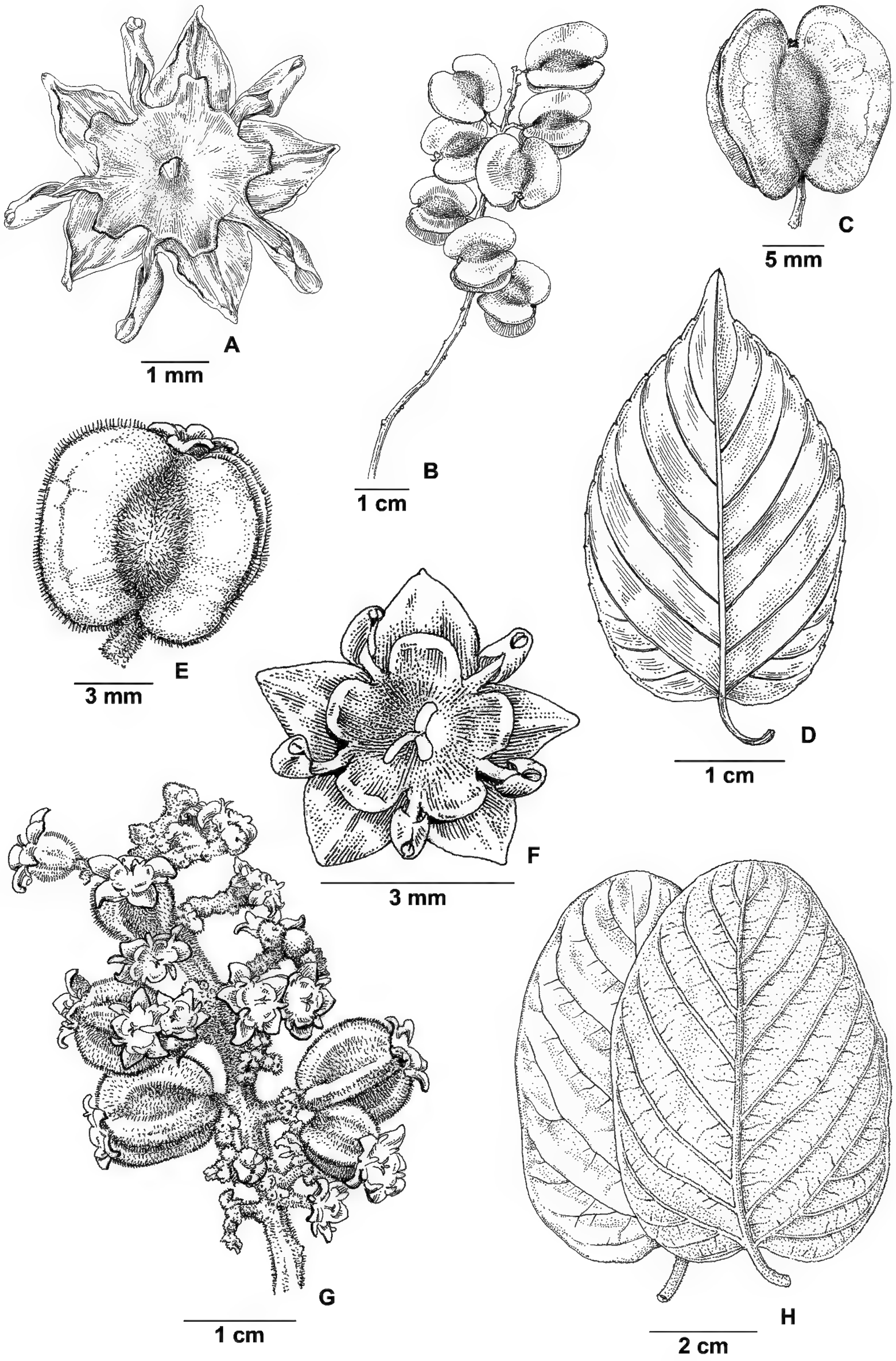


Figure 9. A–D. *Gouania perrieri*. —A. Flower showing the lobes of the disc reaching one fourth of the way along the sepals. —B. Infructescence showing the glabrous fruits concentrated at the base. —C. Fruit. —D. Leaf, abaxial surface. E–H. *Gouania pannigera*. —E. Fruit. —F. Flower showing the lobes of the disc reaching one fourth of the way along the sepal. —G. Inflorescence. —H. Leaf, abaxial surface (in front), adaxial surface (behind). A drawn from *Hildebrandt 3001* (P); B, C from *Hildebrandt 3017* (P); D from *Réserves Naturelles 4228* (P); E–H from *Buerki & Phillipson 35* (TAN).

Discussion. *Gouania pannigera* is morphologically most similar to *G. aphrodes*, *G. mauritiana*, *G. phillipsonii*, and *G. taolagnarensis*, all of which possess leaves with a dense indument and conspicuous tertiary venation on the adaxial surface, and most of which have sessile or shortly pedunculate flowering glomerules. However, *G. pannigera* is distinguished by its ovate leaves, the abaxial surface covered by a whitish or grayish indument and a reddish indument on the veins after drying; peduncle scars left by the flowers; and the presence of glomerules at the base of its infructescence. Furthermore, *G. pannigera* is distributed in the forests and disturbed areas in central Madagascar, whereas *G. aphrodes* is distributed in the north, *G. phillipsonii* is principally distributed in the eastern part of the island, and *G. taolagnarensis* in the southeast.

Perrier de la Bâthie (1943, 1950) treated *Gouania pannigera* as a subspecies of *G. mauritiana* allied to *G. mauritiana* subsp. *aphrodes* (see discussion under *G. aphrodes*) and *G. mauritiana* subsp. *myriocarpa* (see also discussion under *G. myriocarpa*), but we believe that the distinctive suite of characters demonstrated by *G. pannigera*, together with its coherent biogeography and ecological preferences, justify its reinstatement to species rank. *Gouania pannigera* was cited by Engler (1895: 265) from Gorongosa in Mozambique. We have not been able to trace the corresponding herbarium material, but we believe that this was simply a misidentification of a specimen of *G. longispicata* Engl., a form of which is found in that region with a particularly dense indument that resembles that of *G. pannigera*.

Additional specimens examined. MADAGASCAR. **Antananarivo:** Ilafy, *Alleizette 607* (P), *Alleizette 1204* (P); Central Madagascar, *Baron 3971* (K); Tampoketsa d'Ankazobe, PK 120, *Bosser 7808* (TAN); Ambohimanga, *Bosser 12600* (TAN); Soarina, PK 22 rte. de Tananarive, *Bosser 13802* (TAN); Ambohimanga, Colline royale, *Buerki & Phillipson 35* (BR, G, K, MO, NY, P, TAN, US, WAG), *36* (G, K, MO, P, TAN, US, WAG); Ambohimanga, Colline royale, *Buerki & Phillipson 37* (K, MO, P, TAN); Amboasary, bas de la montagne Behenjy, *Buerki et al. 43* (BR, G, K, MO, NY, P, TAN, US, WAG); Ambohimanga, *Decary 667* (P), *Decary 6154* (P), *Decary 6216* (G, P); Anosivato, *Decary 6280* (P); Nord d'Ankazobe, *Decary 7434* (P); Tampoketsa d'Ankazobe, *Decary 19281* (P); Ambohimanga, *Dequaire 27701* (P, TAN); Près d'Amboitromby, *Descoings 3158* (TAN); Rocher d'Iaranandriana, *Dorr et al. 2888* (K, MO, P, TAN, WAG); environs d'Antananarivo, *Goudot s.n.* (G); Ambohimanga, *Herb. Jard. Bot. Tananarive 3262* (P); environs d'Andramasina, *Leandri 3079* (P); Tampoketsa d'Ankazobe, près port forestier de la Manankaza, *Keraudren 1153* (K); Ambohimanga, *Parker s.n.* (K); environs de Betafo, *Perrier de la Bâthie 6013* (P); Ambohimanga, *Perrier de la Bâthie 7057* (P); Mois-Chaîne de Betafo, 1300 m, *Perrier de la Bâthie 13085* (K, P); Forêt d'Ampatsakandrainivavy, *Randrianaivo et al. 518* (MO, P); Ambohitantely PA, *Réserves Naturelles 1222* (P, TAN); Tampoketsa-Ankazobe, *Schatz et al. 3949* (P, TEF); Tsinjoarivo, *Service Forestier (Capuron) 4* (TEF); Andramasina, *Service Forestier 67* (P); Ambohimanga, *Waterlot 57* (P); Ankaratra, *Waterlot 690* (P). **Antsiranana:** Tsaratanana PA, *Réserves Naturelles (Rababoto) 5988* (P). **Fianarantsoa:** Andringitra, N-facing mtn. slopes in N part of Natl. Park, *A. Anderberg, J. Smedmark, B. Axelius, U. Manns & M. Englund 65* (MO, P, S); Soaindrana, *Buerki et al. 49* (BR, G, K, MO, P, S, TAN, US, WAG); Iaritseana, *Buerki et al. 50* (BR, G, K, MO, NY, P, TAN, US, WAG); portion de 5 km anciennement goudronnée en face de la brioche, après Mahasoa, *Buerki et al. 54* (BR, G, K, MO, NY, P, TAN, US, WAG); montée vers le plateau d'Horombe, *Buerki et al. 56* (K, MO, P, TAN); PK 45 rte. Ivato à Ambatofinandrahana, *Cremers 2062* (G, P, TAN); Inselbergs W of Ambalavao, at PK 475 near base of rock formation along creek, *Croat 30187* (MO, TAN, WAG); environs Ambatofinandrahana, *Decary 13172* (P); environs Ambatofinandrahana, *Decary 13260* (P); RN5, Canton Sandrisoa, distr. Ambalavao, *Henri 5532-RN* (P); massif de l'Ivakoany, *Humbert 7037* (P); Ihosy, base de la montée sur l'Horombe, *Jacquemin 1261* (P); Isalo, rivière Sakamalio en aval de l'ancien village, *Jacquemin H352J* (P); Sandrandahy, bassin de la Mania, *Peltier & Peltier 2196* (P); Antanifotsy, forêt de Ramiova et Ambodirina, *Razafindrambao 745* (P); Ambalavao, *Réserves Naturelles (Rabevazaha) 10382* (P); Ranohira, *Service Forestier 13896* (P). **Toamasina:** Menaloha, *Cours 680* (P); Ambatondrazaka, *Decary 16441* (P); rte. de Vohidiale, *Dequaire 27782* (P); ca. 9.5 km au NNW de Didy S rte. Ambatondrazaka, *Gereau et al. 5763* (MO, P); Anony, *Hb. Jard. Bot. Tananarive 2958* (P); Lac Alaotra, *Homolle 580* (P); Ankazotokana, *Réserves Naturelles (Ramanatsoavina) 1954* (P, TAN); Zahamena PA, *Réserves Naturelles 3766* (P); Ankosy, *Rakotovao 11039* (P). **Toliara:** Analavelona, *Andriamihajarivo et al 1656* (MO, P, TAN); limite est de Zombitsy, bord de la Rte. Nat. 7, *Buerki et al. 60* (K, MO, P, TAN); SE, *Descoings 494* (TAN); Forêt d'Analavelona, *Humbert 14231* (P).

13. Gouania perrieri Buerki, Phillipson & Callm., sp. nov. TYPE: Madagascar. Antsiranana: Ankarana PA, 12°56′S, 49°07′E, 100–300 m, 17–24 June 1993 (fr.), *O. Andrianantoanina & R. Bezara 180* (holotype, MO!; isotypes, P!, TAN!), Figure 9A–D.

Gouania glandulosa Boivin ex Tul. var. *sambiranensis* H. Perrier, Notul. Syst. (Paris) 11: 32. 1943, nom. inval.

Haec species a congeneris madagascariensibus foliis glabris cordatis usque deltatis ad marginem leviter crenatis, floribus pedicellis longis (3–7 mm) insidentibus, disci lobis longitudine 1/4 sepalorum partem attingentibus atque fructu magno (ca. 1.5 × 1.5 cm) glabro facile distinguitur.

Woody liana; stems dark green, drying brownish to blackish, glabrous; stipules glabrous, 1(–1.5) × ca. 0.25 mm; tendrils glabrescent. Leaves cordate to deltoid; petioles 10(–20) mm, glabrous; leaf blades (4.5–)5.5(–6) × (3–)4.5 cm; secondary veins alternate, 5 to 6 pairs, not reaching the margin but

following it; conspicuous tertiary veins absent or 2 to 3 pairs present but discrete, arising near the base of the lowest secondary veins, reticulation scalariform discrete; abaxial surface glabrous; midrib, secondary veins, and tertiary veins slightly prominent; adaxial surface glabrous; margin shallowly crenate; base cordate; apex acute to rounded. Inflorescences spindly, lax, glabrescent with hirsute pale trichomes, (3–)7(–9) cm, consisting of glomerules subtended by stipulelike bracts, the proximal flowers developing before the distal flowers; glomerules pedunculate, peduncles accrescent, (1–)3 mm, 2(–4)-flowered; bracts small, densely pubescent on the outer surface with reddish trichomes, glabrous, with a black line on the inner surface, caducous, 0.5(–1) × ca. 0.25 mm; flowers pedicellate, pedicels (3–)4(–7) mm, glabrescent at maturity. Hypanthium obconic, becoming subglobose as the capsule develops; sepals ca. 2 × 0.6 mm, pale yellow, outer surface puberulent, inner glabrous; petals ca. 1 × 0.5 mm, white; stamens slightly longer than the petal blades, with a pale yellow filament and a pale yellow, globose anther ca. 0.2 × 0.2 mm; disc flat, ca. 3 mm diam.; lobes ca. 0.5 mm, emarginate, 1/4 as long as the sepals; stigma with 3 very short linear lobes, style ca. 0.2 mm. Fruits 1 or 2 developing on each glomerule, spheroid, large (ca. 1.5 × 1.5 cm), glabrous, sometimes crenulate on the wings, often aggregated in the proximal part of the infructescence; valves ca. 15 × 10 mm; immature fruits globose, puberulent; seeds brown, shiny, ovoid to pyriform and slightly flattened, ca. 3 × 2 × 0.5 mm.

Distribution and ecology. *Gouania perrieri* occurs in northern and western Madagascar, notably in the Sambirano region (Fig. 2A) in semi-deciduous and evergreen lowland forests on Tsingy limestone and basaltic rocks at an elevational range of 50–500 m.

IUCN Red List category. Based on an EOO of 59,374 km², an AOO of 700 km², and seven subpopulations, four of which occur within protected areas (Ankarana, Montagne d'Ambre, Namoroka), *Gouania perrieri* is thus assigned a preliminary status of Vulnerable (VU B1ab[ii]+2ab[ii]), according to IUCN Red List criteria (IUCN, 2001).

Phenology. The new species has been collected in flower from June to October and in fruit from February to May.

Etymology. This species is named in honor of Joseph Marie Henry Alfred Perrier de la Bâthie (1873–1958), French botanist, geologist, and outstanding explorer of Madagascar for over 30 years.

Discussion. Perrier de la Bâthie (1943) recognized this plant as a variety of *Gouania glandulosa* [≡ *G. scandens* subsp. *glandulosa*], but it differs by the crenulate margins of its leaves, the flowers with long pedicels (vs. sessile), the lobes of the disc reaching one fourth as long as the sepals (vs. the lobes longer, one third to two thirds as long as the sepals), and the large (ca. 1.5 × 1.5 cm) fruits, which are often aggregated on the basal part of the infructescence (vs. ca. 1 × 2 cm and more apically developed). Contrasting also in their distribution, *G. perrieri* is confined to semi-deciduous forest in northern and western Madagascar, while *G. scandens* subsp. *glandulosa* is typical of the humid forest of the east coast. The varietal name provided by Perrier de la Bâthie (1943) was not accompanied by a Latin description or diagnosis and was therefore not validly published according to the ICBN (McNeill et al., 2006: Art. 36.1).

Gouania perrieri is closest to *G. laxiflora* in the size and distribution of the fruits on the infructescence, but can be easily distinguished by the shallowly crenate leaf margins, the long pedicels, the lobes of the disc one fourth as long as the sepals, and its 3-winged immature fruits. It can be distinguished from other species in *Gouania* by its cordiform to deltoid, glabrous leaves with shallowly crenate margins; flowers with long pedicels; the lobes of the disc reaching one fourth as long as the sepals; and the large glabrous fruits concentrated on the basal part of the infructescence. This distinctive suite of characters justifies raising it to species rank.

Paratypes. MADAGASCAR. **Antsiranana:** Ankarana PA, 12°56′S, 49°07′E, *O. Andrianantoanina & R. Bezara 180* (MO, P, TAN); Montagne des Français, 12°19′28″S, 49°20′28″E, *M. Bardot-Vaucaulon 1776* (K, MO, P, TAN); Montagne d'Ambre PA, bord chemin proche camp des Roussettes, 12°31′28″S, 49°10′20″E, *S. Buerki, M. W. Callmander & S. Wohlhauser 1* (MO, P); Bord de la rte. Sambava-Vohemar, PK 53, 13°40′33″S, 50°03′45″E, *Callmander & Wohlhauser 249* (G, K, MO, P, S, TEF); Ankarana PA, 12°51′01″S, 49°13′30″E, *D. K. Harder, M. C. Merello, S. G. Razafimandimbison & T. G. Razafindrabaeza 1750* (MO, TAN); Nosy Be, *J. M. Hildebrandt 3001* (G, P); Norontsanga, [13°55′S, 47°55′E], *J. M. Hildebrandt 3017* (K, P); Ankarana PA, 12°51′S, 49°05′E, *M. Nicoll & J. P. Abraham 678* (K, MO, TAN, WAG); Montagne des Français, [12°20′S, 49°21′E], *H. Perrier de la Bâthie 16322* (P); Amjiabe (Nosy Be), 13°04′50″S, 49°54′07″E, *D. Rabehevitra, R. Razakamalala & T. Rakotomamonjy 226* (MO, P, TEF). **Mahajanga:** Namoroka PA, [16°29′S, 45°20′E], *Réserves Naturelles 4228* (P), *Réserves Naturelles 5620* (P, TAN); Namoroka PA, [16°29′S, 45°20′E], *Service Forestier 3* (P).

14. Gouania phillipsonii Buerki, sp. nov. TYPE: Madagascar. Antananarivo: near Mahasoa, at the base of the Mandraka River, track to the E, 18°55′35″S, 47°55′50″E, 1060 m, 11 Nov. 2001

(fl.), *P. B. Phillipson & G. E. Schatz 5344* (holotype, MO!; isotypes, G!, GRA!). Figure 10.

Haec species ad *Gouaniam pannigeram* Tul. et *G. taolagnarensem* Buerki, Phillipson & Callm. maxime accedit, sed ab eis foliis parvis basaliter rotundatis margine subdenticulato ac venarum secundariarum paribus primo secundoque manifeste separatis, disci lobis longitudine 1/4 sepalorum partem attingentibus atque fructu juventute indumento luteo usque aurantiaco denso maturitate brunneo obtecto distinguitur.

Woody liana climbing to 15 m; stems dark green, drying brown to dark gray, densely pubescent with hirsute reddish brown trichomes; stipules densely pubescent on the 2 faces with reddish brown trichomes, 3(–4) × ca. 1 mm, ± persistent; tendrils pubescent. Leaves broadly ovate; petioles (5–)10–15(–20) mm, pubescent with brown trichomes; leaf blades (2.5–)3.5–4 × (1.5–)2.5 cm, discolorous; secondary veins alternate, the first pair oppositely arranged, 4 to 5 pairs, not reaching the margin but following it, with a larger space between the first and the third pairs, the second pair often reduced; tertiary veins apparent, (3 to)4(to 5) pairs, arising only from the first secondary veins, reticulation scalariform; abaxial surface densely villous with ferruginous to brown trichomes, ± uniform on the limb, midrib, and veins; midrib, secondary veins, tertiary veins, and reticulation prominent; adaxial surface sparsely puberulous with pale brown trichomes, finely bullate resembling reptile skin; margin sparsely denticulate, teeth with a reddish tuft of trichomes; base rounded; apex rounded or subacute. Inflorescences congested, densely pubescent with a reddish indument, (3–)4–7(–12) cm, consisting of glomerules subtended by stipulelike bracts; glomerules pedunculate, peduncles up to 3 mm, (4 to)8-flowered; bracts densely pubescent on both surfaces, persistent, (3–)4 × ca. 2 mm; flowers shortly pedicellate, pedicels up to 1.5 mm, covered by a brown indument. Hypanthium obconic, becoming subglobose as the capsule develops; sepals ca. 2.5 × 1.5 mm, pale yellow, outer surface densely pubescent, inner glabrous; petals ca. 1.5 × 0.75 mm, pale yellow; stamens totally included in the petal blades, with a white filament and a pale yellow, globose anther ca. 0.2 × 0.2 mm; disc flat, ca. 4 mm diam., pale yellow to white; lobes ca. 0.6 mm, thicker than the disc, truncate or somewhat emarginate, 1/4 as long as the sepals; stigma with 3 linear lobes, those ca. 0.3 mm, style ca. 1 mm. Fruits 0 or 1 developing on each glomerule, spheroid (ca. 0.8 × 0.8 cm), covered by a dense brown indument, equally distributed on the infructescence; valves ca. 8 × 4 mm; immature fruits globose, with a dense, pale yellow to orange indument that becomes brown as the fruit matures; seeds pale brown, ovoid and slightly flattened, ca. 3 × 2 × 1 mm.

Distribution and ecology. *Gouania phillipsonii* grows on the eastern escarpment of Madagascar (Fig. 2A) in evergreen montane rainforest, on limestone and lateritic soils at an elevational range of 800–1100 m.

IUCN Red List category. Based on an EOO of 19,298 km², an AOO of 135 km², and nine subpopulations, seven of which occur within protected areas (Andringitra, Anjanaharibe-Sud, Mantadia, Perinet, Ranomafana, Zahamena), *Gouania phillipsonii* is thus assigned a preliminary status of Vulnerable (VU B1ab[ii]+2ab[ii]), according to IUCN Red List criteria (IUCN, 2001).

Phenology. The new species has been noted as flowering from May to November and fruiting from January to March.

Etymology. The species epithet was chosen by the first author in honor of Peter Phillipson (1957–), British botanist and co-author of this article, who made many important collections and observations of Malagasy *Gouania* since his first visit to Madagascar over 20 years ago. He was the co-supervisor of Sven Buerki's M.Sc. research program.

Discussion. Perrier de la Bâthie (1943) was certainly familiar with this plant. He collected it himself at three different localities, citing these together with four other specimens under his *Gouania mauritiana* subsp. *myriocarpa* (Perrier de la Bâthie, 1943: 46). However, he did not see the type specimen, and it is clear that he completely misinterpreted Tulasne's original description of *G. myriocarpa* (see discussion above under *G. myriocarpa*). No existing name is available for the species, which we describe here as new.

Gouania phillipsonii can be distinguished easily by its small broadly ovate leaves, the large space between the first and second pair of secondary veins, the slightly denticulate margin, the abaxial leaf surface with a rather uniform ferruginous to brown indument, and the adaxial surface that is finely bullate, giving it a distinctive aspect reminiscent of reptile skin. The lobes of the disc reach one fourth as long as the sepals, and the immature fruits have a dense yellow indument that becomes brown as the fruits mature.

Gouania phillipsonii is probably most closely related to *G. aphrodes*, *G. pannigera*, and *G. taolagnarensis*, which all have flowers with short disc lobes (less than one fourth the length of the

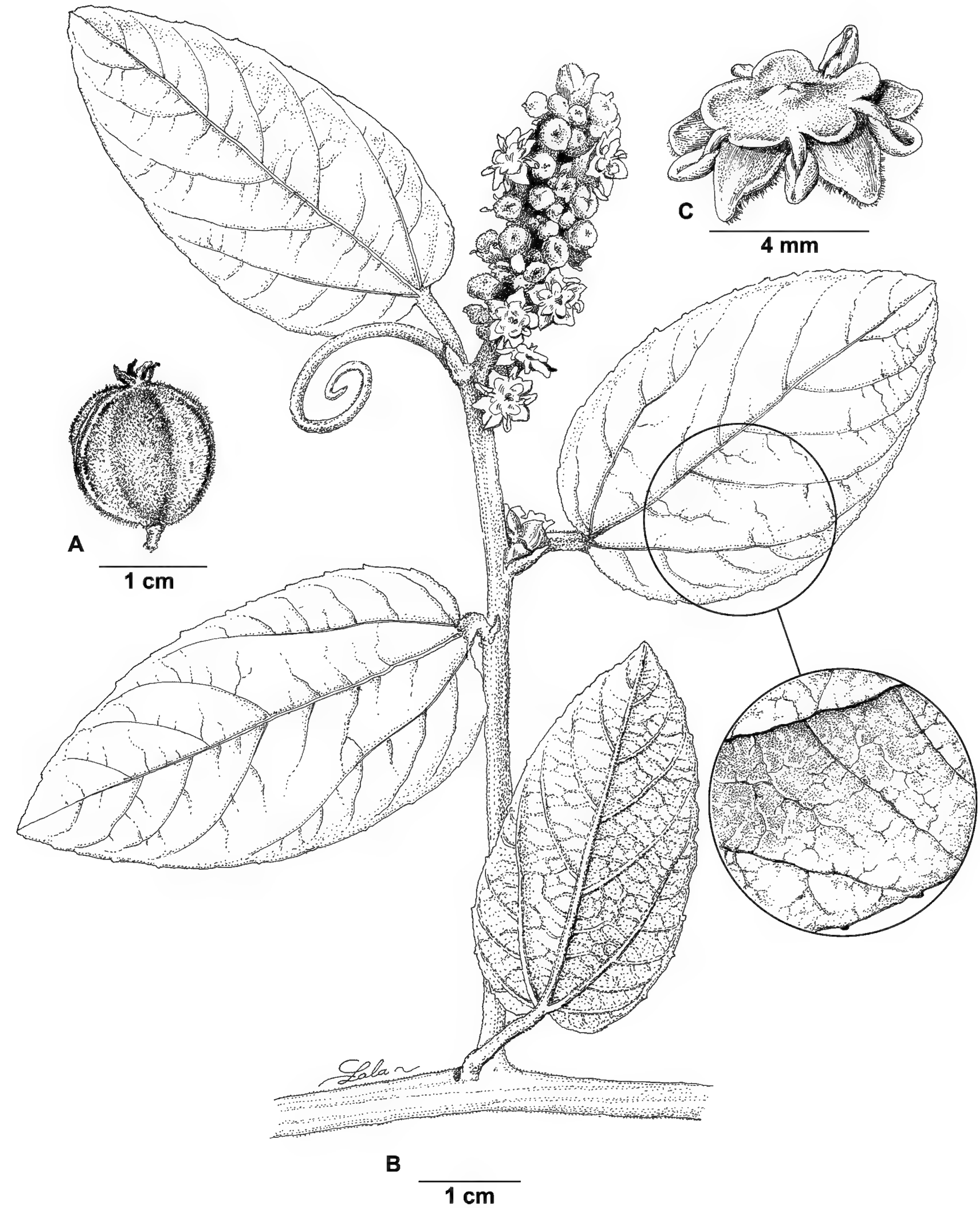


Figure 10. *Gouania phillipsonii*. —A. Fruit. —B. Flowering branch showing the broadly oval leaves with the first and second pairs of secondary veins widely spaced and the reptilian aspect of the adaxial surface. —C. Flower (lobes of the disc reaching one fourth of the way along the sepals). A drawn from *Buerki et al. 42* (TAN); B, C from the type *Phillipson & Schatz 5344* (MO).

sepals) and a relatively dense indument on their leaves. However, despite the diagnostic characters listed above, these species are not sympatric. *Gouania phillipsonii* occurs in forest mainly at mid-elevations on the eastern escarpment of Madagascar, whereas *G. aphrodes* occurs in the north at lower elevations, *G. pannigera* is known from the central region (often in degraded areas), and *G. taolagnarensis* is narrowly endemic to the region of Taolagnaro (Fort Dauphin) in the southeast.

Paratypes. MADAGASCAR. **Antsiranana:** Anjanaharibe-Sud PA, 14°32′45″S, 49°35′15″E, *D. Ravelonarivo 195* (MO, P, TAN). **Fianarantsoa:** Ranomafana, en face du centre VALBIO, 21°15′14″S, 47°25′18″E, *S. Buerki, P. B. Phillipson & C. Rakotovao 47* (G, K, MO, P, TAN); massif de l'Ikongo, [21°51′30″S, 47°26′30″E], *R. Decary 5618* (P); Est Ivohibe, [22°29′S, 46°53′E], *H. Humbert 3383* (G, K, P, TAN); Ranomafana PA, 21°15′S, 47°27′E, *S. Malcomber, A. Leeuwenberg, C. Rakotomazaza, H. L. Raharijaona & G. Rahajasoa 1006* (G, K, MO, P, TAN, WAG); haute Rienana, bassin du Matitana, [22°13′29″S, 46°58′24″E], *H. Perrier de la Bâthie 6022* (P); Ranomafana PA, just S of Namorona River, 21°16′S, 47°25′E, *G. E. Schatz & J. S. Miller 2436* (K, P, TAN, WAG). **Toamasina:** Moramanga, [18°56′S, 48°12′E], *K. R. Afzelius s.n.* (MO, P); Moramanga, Ambatovy, Andasibe, Menalamba, Berano village, 18°50′45″S, 48°15′45″E, *P. Antilahimena & F. Edmond 3956A* (MO, P, TAN); Moramanga, Ambatovy, Andasibe, Menalamba, Ambovy forest, 18°51′38″S, 48°17′28″E, *Antilahimena & Edmond 4088* (MO, P, TAN); Moramanga, Andasibe, Menalamba, rd. Analamay–Ambatovy, 18°50′24″S, 48°19′23″E, *Antilahimena, J. Razanatsoa & Edmond 4219* (MO, P, TAN); Moramanga, Andasibe, Menalamba, Ambatovy forest, 18°51′29″S, 48°18′10″E, *Antilahimena, M. Rabarimanarivo, Razanatsoa & Edmond 4303* (MO, P, TAN); Analamazaotra-Perinet PA, [18°56′S, 48°26′E], *R. Benoist 1507* (P, TAN); Ambatovy, 18°52′10″S, 48°19′09″E, *Buerki, Phillipson & Rakotovao 42* (BR, G, K, MO, P, TAN, WAG); Ambatoharanana, [18°00′S, 48°40′E], *G. Cours 4118* (P); Sahamalaza, près du lac Alaotra, *J.-M. Dequaire 27976* (P); La Mandraka, *Hb. Jard. Bot. Tananarive 4468* (P); entre Mandritsara et Andilamena, *Humbert 18059* (P); Analamazaotra-Perinet PA, [18°56′S, 48°26′E], *M. Keraudren & G. G. Aymonin 25384* (P); near Andasibe, forest of Mantadia, 18°55′S, 48°25′E, *G. McPherson & H. van der Werff 16486* (G, K, MO, P, TAN); forest N of Andasibe, 18°56′S, 48°25′E, *Miller, J. Bradford, F. Rakotonasolo & A. Randrianasolo 8750* (TAN, WAG); River Anove, *H. Perrier de la Bâthie 6016* (K, P, TAN); Analamazaotra-Perinet PA, [18°56′S, 48°26′E], *Perrier de la Bâthie 6055* (K, P, TAN); Antsangimaso, Fokontany Ampitambe, Ambatovy, commune rurale Ambohibary, 18°51′05″S, 48°18′13″E, *Razanatsoa, Antilahimena & Edmond 536* (MO, P, TAN); Moramanga, Ambohibary, Ampitambe, Forêt d'Ambohitavolo, 18°50′49″S, 48°17′17″E, *Razanatsoa, Antilahimena & Edmond 162* (MO, P, TAN); Distr. Moramanga, Commune: Ambohibary, Fokontany: Ampitambe, Ambatovy, environ 22 km NE de Moramanga, 18°51′30″S, 48°18′16″E, *Rakotovao, R. Razafindasy & Edmond 1443* (MO, TAN); Varaina, *Réserves Naturelles 1593* (P); Forêt de Mantadia, 18°52.2′S, 48°29.8′E, *F. L. van Nek 2015* (TAN, WAG).

15. Gouania scandens (Gaertn.) R. B. Drumm., Fl. Zambes. 2: 435. 1966. Basionym: *Retinaria scandens* Gaertn., Fruct. Sem. Pl. 2: 187, tab. 120, fig. 4. 1791. *Retinaria volubilis* Gaertn., Fruct. Sem. Pl. 2: 187, tab. 120, fig. 4. 1791. nom. superfl. *Gouania retinaria* DC., Prod. (DC.) 2: 40. 1825, nom. superfl. TYPE: [Mauritius.] Tab. 120, fig. 4 in Gaertner, 1791: 187 (lectotype, designated by Drummond [1966: 435, tab. 120, fig. 4] in Gaertner [1791: 187]).

Gouania tiliifolia Lam., Encycl. (Lamarck) 3: 5. 1789, as "*tiliaefolia*," non *Gouania tiliifolia* Rottb. ex DC., 1825, nec *Gouania tiliifolia* Roxb., 1795 [= *Gouania microcarpa* DC.]. TYPE: [Réunion Island.] Île Bourbon, s.d. (fl. & fr.), *Commerson s.n.* (lectotype, designated here, P-LA!; isotype, G!).

Woody liana climbing to a height of 15 m; stems dark green, drying brown to blackish, young shoots puberulent to pubescent with brown or red-brown trichomes, glabrous at maturity; stipules triangular to triangular-lanceolate, blackish, glabrous, ca. 3(–4) × (0.75–)2 mm, ± persistent or early caducous; tendrils sparsely pubescent, glabrescent. Leaves ovate to cordate; petioles dark brown, (8–)12–15(–20) mm, hirsute with caducous trichomes; leaf blades (4–)5–6(–8) × (2–)3(–4.5) cm; secondary veins alternately arranged, except the first pair opposite, 4 to 5 pairs, not reaching the margin but following it; tertiary veins apparent, 2 to 5 pairs, reticulation scalariform, conspicuous or not; abaxial surface glabrous or hirsute and glabrescent; adaxial surface glabrous; margin crenulate or entire; base rounded to shallowly cordate; apex acute to subacute. Inflorescences congested, puberulous or hirsute-glabrescent, (5–)7–14(–19) cm; glomerules sessile, lowest glomerules sometimes pedunculate; bracts triangular or lanceolate, glabrous or sparsely pubescent; flowers pedicellate, pedicels 3–5 mm. Hypanthium obconic, becoming subglobose as the capsule develops; sepals 2–2.5 × 0.8–2 mm, puberulent to glabrous outside, glabrous inside; petals 1–1.5 × ca. 0.5 mm, white to pale yellow; stamens about as long as the petals, pale yellow, with globose anther ca. 0.2 × 0.2 mm; disc flat, 3–4 mm diam.; lobes 0.5–1.5 mm, truncate to emarginate, 1/4 to 2/3 as long as the sepals; stigma with 3 linear lobes, 0.2–0.4 mm, style protruding from the disc. Fruits 0 or 1 developing on each glomerule, oblong (1–1.5 × ca. 2 cm), glabrous, with a curved pedicel; seeds pale to medium brown, ovoid and slightly flattened, 3–4 × 2–3 × ca. 0.5 mm.

Distribution and ecology. *Gouania scandens* occurs in Mauritius, Réunion Island, and Madagascar (east coast and Sambirano regions). It grows in evergreen lowland and montane rainforest, on limestone, sand, gneiss, and lateritic soils at an elevational range from sea level to 1100 m.

IUCN Red List category. Within Madagascar, *Gouania scandens* has an EOO of 148,427 km², an AOO of 306 km², and 27 subpopulations, eight of which occur encompassed within protected areas (Andringitra, Anjanaharibe-Sud, Betampona, Marojejy, Masoala, Zahamena). It is thus assigned a preliminary status of Least Concern (LC), in Madagascar according to IUCN Red List criteria

(IUCN, 2001). We have not assessed its conservation status for other countries in which it occurs.

Discussion. Gaertner's (1791) protologue for *Retinaria scandens* consists of no more than the description and illustration of the fruits of a plant collected by P. Hermann in Mauritius. Gaertner's fruits correspond well to those of *Gouania tiliifolia*, but we have failed to find a corresponding specimen in Gaertner's herbarium at TUB and so we have not been able to confirm other characters of the specimen. When Drummond (1966) made the combination *G. scandens*, he lectotypified his new combination on the illustration in Gaertner (Pl. 2: 187, tab. 120, fig. 4. 1791) and included material from mainland Africa. However, we believe that the African material he associated with the name *G. scandens* is conspecific with *G. laxiflora*. The latter is the only known species of *Gouania* shared between mainland Africa and the Indian Ocean islands (see discussion under *G. laxiflora*); *G. scandens* does not occur in mainland Africa.

Gouania scandens is a common species in eastern Madagascar. This species can be confused with *G. myriocarpa*, with which it is partially sympatric and vegetatively similar. However, characters of the flower and fruit allow us to easily distinguish these two species. *Gouania scandens* is characterized by its glabrescent inflorescence (vs. pubescent with hirsute ferruginous trichomes in *G. myriocarpa*) and its rather lax infructescence with large oblong fruits, ca. 2 cm diam. (vs. a condensed infructescence with smaller spheroid fruits, ca. 0.6 cm diam.).

KEY TO THE SUBSPECIES OF *GOUANIA SCANDENS*

1. Leaf generally cordiform or sometimes ovate; margins crenulate; stipules triangular, ± persistent; lobes of the disc highly variable on a single flower (varying from 1/4 to as long as the sepals); Mauritius and Réunion Island ..... 15a. *G. scandens* subsp. *scandens*

1′. Leaf ovate; margins entire, sometimes sparsely crenulate; stipules triangular-lanceolate, early caducous; lobes of the disc only slightly variable on a single flower (varying from 1/3 to 2/3 as long as the sepals); eastern Madagascar ..... 15b. *G. scandens* subsp. *glandulosa*

15a. Gouania scandens (Gaertn.) R. B. Drumm. subsp. **scandens**.

Woody liana; stipules triangular, 3(–4) × ca. 2 mm, ± persistent; tendrils sparsely pubescent at maturity. Leaves ovate to cordate; petioles dark brown, (10–)15(–20) mm, hirsute with caducous ferruginous trichomes; leaf blades (4.5–)5.5(–8) × (2.5–)3(–4.5) cm; tertiary veins few, arising only from the first secondary veins, reticulation not conspicuous; abaxial surface pale green, glabrous; midrib, secondary veins, tertiary veins, and reticulation slightly prominent; margin crenulate, teeth with a black gland; base rounded; apex acute to subacute. Inflorescences hirsute-glabrescent with ferruginous trichomes, (9–)12–14(–16) cm; glomerules peduncu-late at the base, becoming sessile near the apex; bracts triangular, sparsely pubescent with pale ferruginous trichomes on the outer surface and glabrous on the inner surface, 1(–2) × ca. 0.5 mm; pedicels (3–)4(–4.5) mm, densely pubescent with ferruginous trichomes. Sepals ca. 2 × 0.75 mm, pale yellow, outer surface puberulent; petals ca. 1 × 0.5 mm; disc ca. 3 mm diam.; lobes truncate or somewhat emarginate, 1/4 or as long as the sepals; stigma lobes ca. 0.4 mm, style ca. 1 mm. Fruits ca. 1.5 × 2 cm, equally distributed on the infructescence; valves ca. 15 × 10 mm; seeds pale brown, ca. 3 × 2 × 0.5 mm.

Distribution and ecology. *Gouania scandens* subsp. *scandens* occurs on Mauritius and Réunion in evergreen lowland rainforest at an elevational range of 200–600 m.

Phenology. This subspecies has been recorded in flower in January, May, and July and in fruit in April.

Discussion. *Gouania scandens* subsp. *scandens* is endemic to the Mascarenes. It is probably the only *Gouania* native to Mauritius. On Réunion it can easily be distinguished from *G. mauritiana* by its glabrous or at most sparsely pubescent vegetative parts (vs. densely pubescent). Furthermore, *G. scandens* subsp. *scandens* can be recognized by its cordiform, glabrous leaves, the crenulated margins with a black gland at the apex of every crenation, the lobes of the disc from 1/4 to as long as the sepals on the same flower, and the fruits with an arcuate pedicel, which tend to be rather equally distributed on the infructescence.

Additional specimens examined. MAURITIUS. s. loc., *Ayres s.n.* (K); *Bojer s.n.* (K); *Commerson 626* (P); *Commerson s.n.* (K, P); *Sieber fl. Mixta 208* (P); *Sieber s.n.* (G); forêts du quartier du grand Port, *Boivin s.n.* (P); Grand Port, and along the way to Vacoas, *Bouton 5* (K); Long Montane, *Bouton 65* (K); Piton du Fouge, mtn. range (E foot hills of ridge running toward Baie du cap), *Guého 17901* (K, P); Perrier Natl. Reserve near Mare aux Vacoas, *Lorence 2343* (K, MO, P); Bel Ombre Forest above Bon Courage, *Lorence et al. 4494* (MO). RÉUNION ISLAND: s. loc., *Commerson s.n.* (G), *Pourret s.n.* (P), *Richard s.n.* (K). Ville Bague, *Commerson s.n.* (G, P).

15b. Gouania scandens subsp. **glandulosa** (Boivin ex Tul.) Buerki, Phillipson & Callm., comb. et stat. nov. *Gouania glandulosa* Boivin ex Tul.,

Ann. Sci. Nat., Bot. sér. 4, 8: 129. 1857, as "*Guania*." TYPE: Madagascar. Toamasina: Sainte-Marie, 1834 (fr.), *A. Bernier 239* (lectotype, designated here, P!).

Gouania madagascariensis Rich. ex Tul., Ann. Sci. Nat., Bot. sér. 4, 8: 129. 1857, as "*Guania*," nom. inval. (ICBN, Art. 34.1a).

Gouania sulcata Bojer, Hortus Maurit. 71. 1837, nom. nud.

Woody liana; stipules triangular-lanceolate, 3(–4) × ca. 0.75 mm, early caducous; tendrils sparsely glabrous at maturity. Leaves ovate; petioles dark brown, (8–)12–15(–20) mm, hirsute with caducous brown trichomes; leaf blades (4–)5–6(–7) × (2–)3–3.5 cm; tertiary veins apparent, arising near the base of the lowest secondary veins, scalariform reticulation conspicuous; abaxial surface green to dark green, hirsute (and rough to the touch), glabrescent; midrib, secondary veins, and tertiary veins hardly prominent; margin generally entire, sometimes sparsely crenulate near the base and the apex; base rounded to shallowly cordate; apex acute. Inflorescences puberulous with pale pannose trichomes, (5–)7–9(–19) cm; glomerules sessile; bracts lanceolate, glabrous on both surfaces, (2–)2.5 × ca. 0.5 mm; pedicels up to 5 mm, densely puberulent with pale trichomes. Sepals ca. 2.5 × 2 mm, pale yellow to brown, outer surface puberulent to glabrous; petals ca. 1.5 × 0.5 mm, pale yellow; disc ca. 4 mm diam.; lobes emarginate or somewhat truncate, 1/3 to 2/3 as long as the sepals; stigma lobes ca. 0.2 mm, style ca. 3 mm. Fruits ca. 1 × 2 cm, mainly developed at the apex of the infructescence; valves ca. 10 × 10 mm; seeds brown, ca. 4 × 3 × 0.5 mm.

Distribution and ecology. *Gouania scandens* subsp. *glandulosa* occurs in eastern Madagascar and the Sambirano region (Fig. 2C). It grows in evergreen lowland rainforest, on limestone, sand, gneiss, and lateritic soils at an elevational range of (0–)300–800(–1100) m.

Phenology. *Gouania scandens* subsp. *glandulosa* has been noted as flowering from November to April and fruiting from May to October.

Discussion. *Gouania scandens* subsp. *glandulosa* was treated by Tulasne (1857) and Perrier de la Bâthie (1943) as a distinct species, but we consider the similarity of this plant to typical *G. scandens* to be such that they should be regarded as conspecific. After examining the copious amounts of material available for both taxa, we have concluded that the small differences that do exist in the leaves and stipules and the slight differences in the variability in the size of the lobes of the disc are consistently correlated to geographic distribution. The Malagasy specimens can be distinguished from the Mascarene specimens on the basis of these characters, and we believe that subspecies rank is justified for these two allopatric taxa. *Gouania scandens* subsp. *glandulosa* can be distinguished easily from other species in Madagascar by its ovate leaves covered by hirsute caducous trichomes, a dark reticulation on the abaxial surface, the lobes of the disc one fourth to as long as the sepal on the same flower, and large, glabrous fruits concentrated at the apex of the infructescence.

The name *Gouania madagascariensis* appears on labels accompanying Richard's specimens 186 and 335 from Madagascar. It was cited as a synonym of *G. glandulosa* by Tulasne (1857) but was never published as an accepted name, and is therefore nomenclaturally invalid. *Gouania sulcata* was published by Bojer (1837: 71), based on a Boivin collection from Madagascar, but the name lacks an adequate diagnostic description and is regarded as a nomen nudum. We include the Richard and Boivin specimens in question in *G. scandens* subsp. *glandulosa*.

Additional specimens examined. MADAGASCAR. s. loc., fl. & imm. fr., *Baron 1114* (K, P); fl. & imm. fr., *Baron 1443* (K, P); fl., *Baron 2357* (K, P); imm. fr., *Baron 2576* (K, P); "Central Madagascar," *Baron 2713* (K); fl., *Boivin s.n.* (P); fr., *De Lastelle s.n.* (P); fl., 1833, *Goudot s.n.* (G); fl. & imm. fr., *Petit Thouars s.n.* (P); *Humblot 188* (K, P); fl. & fr., *Richard 519* (P). **Antsiranana:** Masoala PA, Sahamalaza-Anovandrano, *Bernard 137* (MO); massif of Tsihomanaomby, *Birkinshaw 731* (P); Masoala PA, *Cours 2199* (P, TAN); Daraina, forêt de Antsahabe, *Gautier 4743* (G, MO); Baie de Diego-Suarez, *Goudot s.n.* (G); Vallée de la Lokoho (Nord-Est), *Humbert 23243* (P); Vallée de l'Antsahabe, *Humbert 23322* (P); Marojejy PA, *Miller & Lowry 3892* (K, MO, P, TAN); Nossy-Mitsiou, *Perrier de la Bâthie 18786* (P); Ambato, *Rabenantoandro & Antilahimena 19* (P); Embouchure d'Ambohitralanana, presqu'île de Masoala, *Rahajasoa 304* (P, WAG); Andapa, Anjiavabe, *Rakotovao 3722* (MO, P, TAN); Marojejy PA, *Rasoavimbahoaka 345* (K, MO, P, TAN); Anjanaharibe-Sud PA, *Ravelonarivo et al. 776* (P, TAN); Ambondrobe, *Razakamalala 1033* (P); Sambava, Bevontro, Tsaratanana, Morafeno, Forêt d'Antsahandroboka, *Razakamalala et al. 3095* (MO, P, TAN); Marojejy PA, *Réserves Naturelles 3954bis-RN* (TAN); Ambohitralana, distr. Antalaha, Masoala PA, *Réserves Naturelles 4446-RN* (P, TEF); Vohemar, *Richard 251* (P), *Richard 335* (G, P); Marojejy PA, *Service Forestier 17698-SF* (P, TEF); Anjaniharibe-Sud PA, *Tosh et al. 364* (G, BR, MO). **Fianarantsoa:** Mananjary, *Geay 7234* (P), *Geay 7366* (P, TAN), *Geay 7367* (P), *Geay 7368* (P), *Geay 7694* (P), *Geay 7723* (K, P); Ambalavao, *Réserves Naturelles 8123-RN* (P, TAN). **Toamasina:** Maraontsetra: Ambanizana, *Antilahimena et al. 1079* (MO, P, TAN); St-Marie, *Bernier 268* (P), *Boivin 1881* (P); PK 23 rte. de Tamatave, *Bosser 13760* (MO, TAN); Fotimavo, *Buerki 130* (G, K, MO, P, TAN); Nosy Mangabe, *Carlson 180* (K, P, TAN); Antokazo, *Cours 288* (P); Forêt d'Ambatosoratra, *Cours 3375* (P, TAN); Brickaville, *D'Arcy 15281* (K, MO); Fenerive, *Decary 3907* (P, TAN); Ambila, *Decary 6310*

(K, P), *Decary 6397* (P); Zahamena PA, *Decary 16798* (P); Mangabe, *Decary 16872* (K, P); Mahavelona (Foulepointe), *Decary 16969* (P), *Decary 16983* (P); Lac Alaotra, *Herb. Jard. Bot. Tananarive 4307* (P); Rendrirendry, 17°55′S, 049°13′E, *Iambana et al. 137* (P); Maroantsetra, *Leeuwenberg 13941* (MO, P, TAN, WAG); Masoala PA, *Nicoll et al. 554* (K, MO, P, TAN, WAG); St-Marie, *Pervillé 231* (P); environs du confluent de l'Onive et du Mangoro, *Perrier de la Bâthie 17150* (P); bord de l'Onive près Antanandavohily-Antalaha, *Rakotozafy 517* (TAN); Zahamena PA, *Réserves Naturelles 4947-RN* (P), *Réserves Naturelles 7260-RN* (P), *Réserves Naturelles 10663-RN* (P), *Réserves Naturelles 10881-RN* (P); Betampona RN, *Réserves Naturelles 3954-RN* (P, TAN); Fenerive, *Réserves Naturelles 7840-RN* (P); Sahamalaza, *Réserves Naturelles (Laibosaka) 12603-RN* (TAN); Androrangabe, *Réserves Naturelles (Laibosaka) 12614-RN* (TAN); St-Marie, Antongil, *Richard comm. 186* (P); Ambahy Forest, ca. 20 km S of Nosy Varika, *Rogers 283* (MO, P). **Toliara:** Prov. Tuléar, *Poisson 180* (P); entre le rite de l'hombre et Fort-Dauphin, *Rabevohitra 2230* (K, MO, P, TAN).

16. Gouania taolagnarensis Buerki, Phillipson & Callm., sp. nov. TYPE: Madagascar. Toliara: Com. Manambaro, 3 km O de Manambaro, bord de la RN13, 25°01′44″S, 46°46′51″E, 14 m, 23 Mar. 2005 (fl. & imm. fr.), *S. Buerki & P. B. Phillipson 68* (holotype, MO!; isotypes, BR!, G!, K!, NY!, P!, TAN!, US!, WAG!). Figure 11.

Haec species a congeneris madagascariensibus foliis ovatis usque cordatis ad basem asymmetricis venulis quaternariis praeditis, inflorescentia floribusque indumento pallide fusco obtectis atque fructibus secus inflorescentiam ad partem distalem congestis juventute indumento pallide luteo vestitis deinde rubescentibus quaque ala in centro lineis transversalibus duabus vel tribus notata facile distinguitur.

Woody liana climbing to 10 m; stems dark green, drying brown, densely pubescent with a brown indument; stipules pubescent on the 2 faces with brownish trichomes, (2–)3(–4) × ca. 1 mm, caducous; tendrils pubescent. Leaves ovate to cordate; petioles (8–)10–15 mm, densely pubescent with a brown trichome; leaf blades 4–5(–6) × (2.5–)3–3.5 cm, discolorous; secondary veins alternate, 6 to 7 pairs, reaching and following the margin; tertiary veins apparent, 4 to 7 pairs, arising near the base of the lowest secondary veins and sometimes in the upper part, quaternary veins arising from the first tertiary veins, reticulation scalariform; abaxial surface villous with whitish to pale brown trichomes; midrib, secondary, tertiary, and quaternary veins prominent; adaxial surface sparsely pubescent with pale brown to whitish trichomes; margin sparsely crenulate from the base to the apex; base of the young leaves rounded, cordate and asymmetric on mature leaves; apex generally rounded, sometimes subacute. Inflorescences ± congested, densely pubescent with a pale brownish indument, (6–)10–15(–20) cm, accrescent, the proximal flowers developing before the distal flowers; glomerules generally sessile, basally pedunculate, up to 5-flowered; bracts lanceolate, densely pubescent on both surfaces with a brownish indument, ± persistent, 3(–4) × ca. 1 mm; flowers shortly pedicellate, pedicels up to 1 mm, pubescent with brownish to silver trichomes. Hypanthium obconic, becoming subglobose as the capsule develops; sepals ca. 1.25 × 1 mm, pale yellow, outer surface densely pubescent with silver trichomes, inner glabrous; petals ca. 1 × 0.2 mm, white; stamens totally included in the petal blades, with a white filament and a pale brown, globose anther ca. 0.2 × 0.2 mm; disc flat, ca. 2 mm diam., yellow becoming white with age; lobes ca. 0.2 mm, thicker than the disc, truncate, 1/6 as long as the sepals; stigma with 3 linear lobes, those ca. 0.5 mm, style ca. 1.5 mm. Fruits 0 or 1 developing on each glomerule, spheroid (ca. 1.2 × 1.2 cm), densely pubescent with reddish trichomes, which become brownish after drying, those reaching maturity mainly distributed in the distal part of the infructescence; valves ca. 1.2 × 1.2 cm; immature fruits globose, with a pale yellow indument, with 2 or 3 transverse lines on the center of the wing; seeds pale black, ovoid and slightly flattened on the inner surfaces, ca. 4 × 2.5 × 1 mm.

Distribution and ecology. *Gouania taolagnarensis* is restricted to southeastern Madagascar in the Taolagnaro region (Fort Dauphin) (Fig. 2C). It grows in evergreen lowland to montane rainforest, sometimes in the transition to xerophytic vegetation and in secondary forest on granite, gneiss rock types, and on lateritic soils at an elevational range from sea level to 1000 m.

IUCN Red List category. With an EOO of about 12,719 km², an AOO of 108 km², and only seven subpopulations, three of which occur within protected areas (Andohahela, Zombitsy), *Gouania taolagnarensis* is thus assigned a preliminary status of Vulnerable (VU B1ab[ii]+2ab[ii]), according to IUCN Red List criteria IUCN, 2001).

Phenology. The new species has been collected in flower from October to January and in fruit in February and March.

Etymology. The epithet of the new species refers to its endemic locale, in the forests around Taolangaro, Toliara Province.

Discussion. *Gouania taolagnarensis* can be easily distinguished from other species by its ovate to

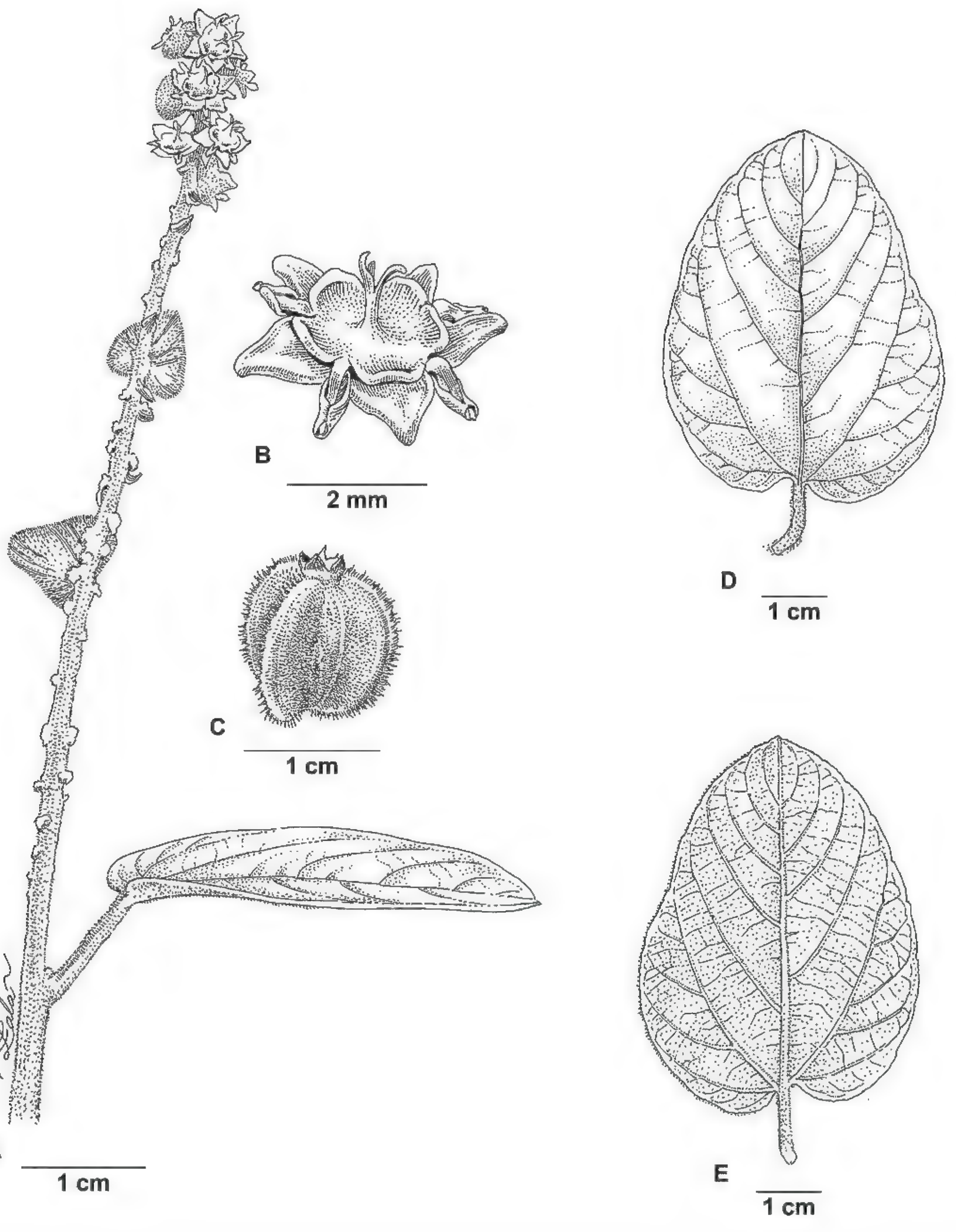


Figure 11. *Gouania taolagnarensis*. —A. Fruiting branch showing immature fruits concentrated mainly in the distal part of the infructescence. —B. Flower showing the lobes of the disc reaching one sixth of the length of the sepals. —C. Fruit showing the two or three transversal veins on the center of each wing. —D. Leaf, adaxial surface. —E. Leaf, abaxial surface, showing the asymmetric limb and the quaternary veins that are particularly well developed on the larger lobe. A–E drawn from *Buerki & Phillipson 64* (TAN).

cordate leaves, the asymmetric base of the blade, the presence of quaternary veins, the pale brown indument that covers the inflorescence and the flowers, immature fruits with a pale yellow indument that reddens with maturity, fruits with two or three transverse lines on the center of the wings, and the fruits concentrated at the distal part of the infructescence.

Gouania taolagnarensis is morphologically most similar to *G. pannigera* in the length of the lobes of the disc and the size and pubescence of the fruits, but differs in having ovate to cordate leaves, the margin of

the apex slightly crenulate, an asymmetric blade, quaternary veins well developed in the asymmetric portion, the inflorescence with a brownish indument, the immature fruits with a yellow indument, those reaching maturity becoming reddish mainly distributed in the distal part of the infructescence. Furthermore, *G. taolagnarensis* appears to be endemic to the region near Taolagnaro (southeastern Madagascar), whereas *G. pannigera* is confined to the forests and disturbed areas of central Madagascar.

Paratypes. MADAGASCAR. **Toliara:** Ambinanibe, 25°02′31″S, 46°55′31″E, *S. Buerki & P. B. Phillipson 64* (BR, G, K, MO, NEU, P, TAN, US, WAG); Fort-Dauphin, Vahapinsouran, *J. Cloisel 94* (P); Chaine Anosyennes from Fort-Dauphin to Ranamafona, [24°25′S, 46°58′30″E], *T. B. Croat 31765* (MO, TAN, WAG); Col de Maningotry, [26°42′S, 46°44′30″E], *N. Dumetz 1275* (MO, P, TAN); Andohahela PA, 24°47′S, 46°52′E, *J. J. Floret, P. P. Lowry II, A. M. J. Leeuwenberg & R. Rajemsa 1968* (MO, P [2]); bassin de réception de la Mananara, pentes occidentales des montagnes entre Andohahela et l'Elakelaka, [24°45′S, 46°44′E], *H. Humbert 13949* (P); Forêt de Manantantely, [24°59′S, 46°55′E], *Humbert 20368* (P); Baie des Galions (Ranofotsy), [25°09′S, 46°43′E], *Humbert 28976* (P); RN7 at 15 km NE of Sakaraha, [22°56′S, 44°33′E], *D. Lorence 2098* (K, MO); Andohahela PA, 24°38′S, 46°46′E, *S. T. Malcomber, H. van der Werff, C. Hemingway, M. van Bergen, S. Rapanarivo, P. J. Rakotomalaza, O. Andrianantoanina & B. Randriamampionona 2184* (P, TAN); Manasoa, *M. Ramarokoto 2100-RN* (P, TAN); Andohahela PA, [24°40′S, 46°48′E], *Ramarokoto 5018-RN* (P, TAN); Andohahela PA, 24°40′S, 46°48′E, *B. Randriamampionona 14* (MO, P, TAN, WAG); Andohahela PA, parcelle 1, 24°40′S, 46°48′E, *Randriamampionona 92* (MO, P, TAN, WAG); Fort-Dauphin, *W. Rauh 1265* (TAN); Distr. Fort-Dauphin, *Réserves Naturelles 8584* (P, TAN); Fort Dauphin, *M. Scott-Elliott 2568* (K, P).

17. Gouania zebrifolia Buerki, Phillipson & Callm., sp. nov. TYPE: Madagascar. Antsiranana: Sahafary, 12°34′42″S, 49°27′16″E, 215 m, 22 Feb. 2006 (fl.), *C. Birkinshaw, M. Andrianjafy & R. Guittou 1563* (holotype, MO!; isotypes, CNARP!, K!, P!, TAN!). Figure 3B–D.

Haec species a congeneris madagascariensibus foliis membranaceis orbicularibus usque reniformibus abaxialiter indumento tenui albo vestitis, venis tertiariis atris crassis reticulum scalariforme formantibus, margine denticulato quoque dente in caespitem trichomatum brunneolorum desinente atque disci lobis longitudine 1/2 sepalorum partem attingentibus facile distinguitur.

Woody liana climbing to 15 m; stems drying brown, finely pubescent to villous with brownish trichomes; stipules villous with brownish trichomes on the upper surface and glabrous on the inner surface, 3(–4) × ca. 1 mm; tendrils pubescent. Leaves orbicular to reniform; petioles (5–)10(–15) mm, pubescent with brownish trichomes; leaf blades 3.5–4.5(–6) × 3.5(–5) cm, membranous; secondary veins alternate to subalternate, 6 to 7 pairs, reaching and following the margin; conspicuous tertiary veins apparent, arising near the base of the lowest secondary veins, this reticulation scalariform, blackish; abaxial blade surface pubescent with fine white trichomes; midrib, secondary, and tertiary veins prominent; adaxial surface sparsely pubescent with white trichomes; margin denticulate to crenulate, with a tuft of brownish trichomes on every tooth; base rounded to shallowly cordate; apex rounded to acute. Inflorescences ± congested, villous with brownish trichomes, (3–)4–4.5(–5.5) cm, consisting of glomerules subtended by stipulelike bracts; glomerules sessile, 4- to 5(to 8)-flowered; bracts triangular-lanceolate, densely pubescent with villous brownish trichomes on the outer surface, glabrous on the inner, ± persistent, (3–)4.5 × ca. 0.5 mm; flowers shortly pedicellate, pedicels to ca. 1 mm, pubescent with villous whitish indument, apparently protandrous. Hypanthium broadly obconic, becoming subglobose as the capsule develops; sepals ca. 0.8 × 0.5 mm, reddish to brown, outer surface villous, inner glabrous; petals ca. 0.75 × 0.2 mm, brownish; stamens slightly longer than the petal blades, with a pale brown filament and a pale yellow, globose anther ca. 0.2 × 0.2 mm; disc flat, ca. 2 mm diam., dark blue when dry; lobes ca. 0.4 mm, thinner than the disc, emarginate or somewhat truncate, 1/2 as long as the sepals; stigma with 3 linear lobes, those ca. 0.4 mm, style ca. 0.6 mm. Immature fruits globose, villous with brownish trichomes; mature fruit not seen.

Distribution and ecology. *Gouania zebrifolia* is endemic to northeastern Madagascar and only known from a few localities in Antsiranana: Loky-Manambato (Daraina), Sahafary, and Montagne des Français (Fig. 2A). The new species grows in semi-deciduous forest at an elevational range of 50–300 m.

IUCN Red List category. With an EOO of about 631 km², an AOO of 36 km², and only three subpopulations, none of which occur within a protected area, *Gouania zebrifolia* is assigned a preliminary status of Endangered (EN B1ab[ii]+2ab[ii]), according to IUCN Red List criteria (IUCN, 2001).

Phenology. This species has been collected in flower and with immature fruits in March.

Etymology. This species is named for the unusual dark patterning of darker stripes on a pale

blade background formed by the blackish reticulation of the tertiary veins.

Discussion. *Gouania zebrifolia* can be recognized easily by its orbicular to reniform, membranous leaves covered by fine white indument on the abaxial surface, which contrasts with the conspicuous blackish scalariform reticulation, with a tuft of brown trichomes on each marginal tooth, and the immature fruits villous with brown trichomes. The taxon shares with *G. ambrensis* the character of disc lobes that are about one half as long as the sepals.

Paratypes. MADAGASCAR. **Antsiranana:** Montagne des Français, 12°19′27″S, 49°20′16″E, *M. Bardot-Vaucoulon & G. Véné 1635* (K, MO, P, TAN); Daraina, forêt d'Ambilondamba, 13°09′S, 49°39′E, *L. Gautier, S. Wohlhauser & L. Nusbaumer 4263* (Herbier de Recherche de Daraina, G, K, MO, P, TEF); Forêt de Sahafary entre Diego et Anivorano, [12°33′S, 49°28′E], *M. Keraudren 1667* (P); Daraina, forêt de Bekaraoka, 13°11′S, 49°42′E, *P. Ranirison & Nusbaumer 957* (Herbier de Recherche de Daraina, G, K, MO, P, TEF); Andriafiabe Commune, Sahafary Forest, ca. 6 km W of Saharenana, Sahafary, 12°35′S, 49°26′59″E, 222 m, *J. Wen, J. Razafitsalama & H. Tombondray 9557* (MO, US).

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PHYLOGENETIC INFLUENCE ON TWINING CHIRALITY IN LIANAS FROM AMAZONIAN PERU[1]

Robyn J. Burnham[2] and Caissa Revilla-Minaya[3]

Abstract

A majority of angiosperm species of vines and lianas use their stem apices for twining and adherence to support structures. Prior observations have suggested a strong predominance of twining orientation in a dextral (right-handed) direction. We present here the chirality of twining (handedness) for 60 taxa representing 21 families encountered in a terra firme Amazonian forest community in Peru. We surveyed 145 stems of climbers that represented one to eight individuals of a given taxon. We demonstrate that dextral chirality is phylogenetically widespread among angiosperm stem climbers and suggest that phylogenetic deviations from the dextral pattern represent independent evolutionary events. Phylogenetic constraint might be invoked to explain the dextral dominance among climbers, but dextral circumnutation is not ubiquitous in other angiosperm organs. Here we also clearly define climbing chirality because of the confusion in previous literature, and we compile published family-level reports of deviations from dextral orientation. This study underscores the need for approaching the twining chirality of plants from genetic, developmental, and physiologic perspectives to clarify the basis for the preferred twining orientation among angiosperm climbers.

Resumen

La mayoría de las especies de lianas y enredaderas angiospermas utilizan los ápices de sus tallos para enredar y adherirse a las estructuras que les sirven de soporte. Observaciones empíricas muestran una marcada preferencia por una dirección de enrollamiento destral (hacia la derecha). Presentamos a continuación la dirección de quiralidad preferida por 60 especies de 21 familias de plantas trepadoras encontradas en un bosque Amazónico de tierra firme en Perú. Evaluamos 145 tallos de trepadoras que representaron entre uno y ocho individuos de cada morfotipo. Nos demostramos que la quiralidad destral está ampliamente distribuida filogenéticamente entre las angiospermas trepadoras y sugerimos que desviaciones filogenéticas del patrón destral representan eventos evolutivamente independientes. Las restricciones filogenéticas pueden explicar la dominancia destral entre trepadoras, pero el quiralidad destral aparentemente no es omnipresente entre otros órganos de angiospermas. En este estudio también definimos claramente la quiralidad de trepar debido a la confusión en previos trabajos, y recopilamos reportes publicados a nivel de familias sobre desviaciones de la quiralidad destral. Este estudio resalta la necesidad de enfocar la dirección de enrollamiento de las plantas desde las perspectivas genética, del desarrollo, y fisiológica para aclarar el origen de la preferencia de dirección de enrollamiento en las angiospermas trepadoras.

Key words: Amazonia, chirality, dextral, handedness, liana, Los Amigos, Peru, sinistral, twiner, vine.

Climbing plants (vines and lianas) ascend using the structural support of a host plant or structure. Mechanisms and organs used for attaching to and climbing a host include twining stem apices, tendrils (axillary, petiolar, or leaf), spines, adventitious roots, stem-derived hooks, and simple scrambling. Although the mechanism employed for ascent can vary, within most families only one mechanism is normally found. For example, almost all climbing species of Bignoniaceae ascend using tendrils modified from the terminal leaflet of a trifoliate leaf; almost all species of Apocynaceae climb by twining stems; the climbing Celastraceae generally use either touch-sensitive axillary branches (Hippocrateoideae and Salicoideae) or stem twining (Celastreae); and most Cucurbitaceae and Passifloraceae climb using axillary determinate stems modified as coiling tendrils. One exception is the large legume family, Fabaceae, in which almost all types of climbing mechanisms can be found.

Table 1 summarizes the primary climbing mechanism of Neotropical climbers from 49 families based on our observations from field sites in Amazonia and literature reviews (see Table 1 for sources). Few families exhibit more than one strategy for climbing, suggesting that climbing mechanism is strongly correlated with phylogeny (Hegarty, 1991; Ornduff,

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2004; Jongkind, 2005). The largest number of climber families ascend by means of circumnutating apices (hereafter termed "twiners"), which appears to be a recurrent evolutionary innovation that has arisen repeatedly in angiosperms, as noted by Darwin (1876).

Normally twiners do not produce tendrils of any sort, thus achieving their upward movement by strong apical helices (axial tension) and frictional force (normal distributed load) on the support structure (Bell, 1958; Silk & Hubbard, 1991; Scher et al., 2001; Silk & Holbrook, 2005). Although the circumnutating stem has its movement arrested at the point of contact with the support, its free apical portion continues circumnutating in the same direction and thus continues upward, wrapping around the support. Interestingly, it has been mentioned by several authors that almost all twiners circumnutate in the same direction (dextrally), and almost all individuals of a species in the same direction (Sachs, 1882; Cribb, 1985; Ornduff, 1991; Hashimoto, 2002; Ford & Purrington, 2004; Lubkin, 2004). Etien and Traoré (2005) reported that 85% of the liana stems encountered in an African forest were dextrally twining, although their data on twining orientation were not published at the species level.

The physiological or anatomical basis for this consistent twining chirality has not been determined, to our knowledge, but has attracted attention from systematists, physicists, physiologists, and mathematicians. Circumnutation itself is caused by a wave of cell elongation on one side of the young internode, and this wave migrates around the stem, causing the bending on the opposite side (Darwin, 1876; Darwin & Darwin, 1881). At the physiological level, the bending is caused by water imbalance on one side of the stem where it causes cells to increase their turgidity and elongate (Lubkin, 2004). To explain circumnutation, different authors have suggested roles for phototropism (Sachs, 1882), thigmotropism (Darwin & Darwin, 1881), geotropism/gravitropism (Israelsson & Johnsson, 1967; Kitazawa et al., 2005), microfibril orientation in xylem (Silk & Hubbard, 1991; Ford & Purrington, 2004), microtubule orientation in cells (Thitamadee et al., 2002; Edwards et al., 2007), epidermal cell anisotropism (Hashimoto, 2002), and anatomical asymmetry (Silk & Hubbard, 1991; Lubkin, 2004; Bowling & Vaughn, 2009). Whatever the ultimate cause, it is clear that once a circumnutating vine begins to twine in a specific orientation, it almost always continues that trajectory, maintaining friction and external pressure against its support, which allows for its ascent (Putz & Holbrook, 1991; Silk & Holbrook, 2005). A complete biological explanation for the mechanism of apical twining must also involve the widespread predominance of dextral twining orientation. Chirality has been observed in a variety of other plant organs (hypocotyls, coleoptiles, roots, petioles, petals, wood), but a predominant chirality across all organs (Hashimoto, 2002; Säll, 2002; Kitazawa, 2005; Mugnal, 2007) has not been observed, to our knowledge.

During fieldwork in Amazonian Ecuador and from casual observations in Peru, Brazil, Bolivia, and the eastern United States, the first author observed that most species of twiners circumnutate dextrally. This led to observations in a variety of field sites, in which it was observed that latitude did not influence the predominance of dextral circumnutation (see also Ornduff, 2004; Edwards et al., 2007).

Here we define circumnutation in three congruent ways to facilitate comparisons with data that exist in the literature (Fig. 1; Table 2). Dextral circumnutation is defined as circumnutation from left to right when observing the upward route of the vine on the support, and conversely sinistral circumnutation is a route from right to left. These terms are equivalent to clockwise and counterclockwise, respectively, when observing the vine from the base of the stem upward, which takes into account the frame of reference taken by the apex of the plant. Darwin's (1876) observations on climbing orientation in vines were recorded as those that move against the sun versus those that follow the sun (dextral and sinistral, respectively). So, counterclockwise (CCW) is equivalent to right to left and to follows the sun. Twining chirality is also referred to in the literature as handedness, with dextral being right handed and sinistral left handed (Kihara, 1972; Ornduff, 1991, 2004; Ford & Purrington, 2004). The simple use of clockwise and CCW (or anticlockwise) is misleading, as this can be differently interpreted whether the climber is viewed from the base of the stem upward, or from the apex downward. Thus, the perspective of observation should always be included where these terms are used (see Allard, 1947; Ornduff, 1991, 2004; Larson, 2000; Edwards et al., 2007 for reports on handedness in which they took the point of reference as from above the stem, and thus their CCW should be clockwise by the system detailed here). We strongly recommend the use of the right-handed and left-handed terms (or dextral/sinistral). As a final note, a convention that never seems to have gained acceptance is the encyclopedic work of Baillaud (1962: 660), who invoked the terms positive and negative for what we designate here as dextral and sinistral, respectively. Kihara (1972) presented a

Table 1. Primary climbing mechanism found in species of 49 families of tropical plants. All mechanisms are based on field observations from Costa Rica, Ecuador, Peru, and Brazil (noted as RJB, pers. obs., only in cases of sole source), in addition to literature sources as cited below. Most families include only one type of climbing mechanism.

Family	Stem twining	Axillary tendrils: stem/inflorescence modification	Tendrils: modified leaf and petiole	Spines/tendrils: modified stipules	Root climbing	Thorny/spiny stems and scramblers	Literature source
Acanthaceae	X						Darwin, 1876; Baillaud, 1962; Ornduff, 2004
Apocynaceae	X						Darwin, 1876; Baillaud, 1962; Ornduff, 2004; Livshultz et al., 2007
Aristolochiaceae	X						Darwin, 1876; Sachs, 1882; Baillaud, 1962; Ornduff, 2004
Asteraceae	X						Darwin, 1876; Baillaud, 1962; Ornduff, 2004
Basellaceae	X						Ornduff, 2004
Boraginaceae	X						Baillaud, 1962; DeWalt et al., 2000; Ornduff, 2004
Caprifoliaceae	X						Darwin, 1876; Larson, 2000; Ornduff, 2004
Celastraceae	X	X					Croat, 1978; Ornduff, 2004; RJB, pers. obs.
Combretaceae	X						Darwin, 1876; Baillaud, 1962; Ornduff, 2004
Connaraceae	X	X					Acevedo-Rodríguez, 2005; RJB, pers. obs.
Convolvulaceae	X						Darwin, 1876; Baillaud, 1962; Ornduff, 2004
Dichapetalaceae	X	X					Hegarty & Caballé, 1991; Jongkind, 2005
Dilleniaceae	X						Darwin, 1876; Baillaud, 1962; Ornduff, 2004
Dioscoreaceae	X						Baillaud, 1962; Hegarty & Caballé, 1991; Ornduff, 2004
Euphorbiaceae	X						Baillaud, 1962; Putz, 1984; Ornduff, 2004
Fabaceae	X	X	X	X	X		Darwin, 1876; Baillaud, 1962; Lewis, 1987; Ornduff, 2004; Acevedo-Rodríguez, 2005
Gnetaceae	X						Carlquist, 1996; Ornduff, 2004
Icacinaceae	X						Ornduff, 2004
Lamiaceae	X						Darwin, 1876; Ornduff, 2004
Malpighiaceae	X						Baillaud, 1962; Hegarty & Caballé, 1991; Ornduff, 2004
Menispermaceae	X						Baillaud, 1962; Hegarty & Caballé, 1991; Ornduff, 2004
Olacaceae	X						RJB, pers. obs.
Piperaceae	X				X		Hegarty & Caballé, 1991; Pinard & Putz, 1994; RJB, pers. obs.

Table 1. Continued.

Family	Stem twining	Axillary tendrils: stem/inflorescence modification	Tendrils: modified leaf and petiole	Spines/tendrils: modified stipules	Root climbing	Thorny/spiny stems and scramblers	Literature source
Polygonaceae	X	X					Sachs, 1882; Baillaud, 1962; Putz, 1984; DeWalt et al., 2000; Ornduff, 2004
Rubiaceae	X			X		X	Darwin, 1876; Hegarty & Caballé, 1991; Putz & Holbrook, 1991; Ornduff, 2004
Verbenaceae	X						Baillaud, 1962; Putz, 1984; Ornduff, 2004
Violaceae	X						Baillaud, 1962; RJB, pers. obs.
Annonaceae		X					Johnson, 2003
Cucurbitaceae		X					Gerrath et al., 2008
Hernandiaceae			X				Ribeiro et al., 1999
Loganiaceae		X					Putz & Holbrook, 1991
Passifloraceae		X					Hegarty & Caballé, 1991
Polygalaceae		X		X			Acevedo-Rodríguez, 2005; RJB, pers. obs.
Rhamnaceae		X					Acevedo-Rodríguez, 2005
Sapindaceae		X					Acevedo-Rodríguez, 2005
Ulmaceae		X					Acevedo-Rodríguez, 2005
Vitaceae		X			X		Hegarty & Caballé, 1991; DeWalt et al., 2000; RJB, pers. obs.
Arecaceae	X						Croat, 1978; Hegarty & Caballé, 1991
Bignoniaceae	X						Hegarty & Caballé, 1991
Ranunculaceae	X						Acevedo-Rodríguez, 2005
Smilacaceae			X				Pinard & Putz, 1994; Acevedo-Rodríguez, 2005
Anacardiaceae				X			RJB, pers. obs.
Araceae				X			Hegarty & Caballé, 1991
Araliaceae				X			Metcalfe, 2005
Begoniaceae				X			Sands, 2009
Hydrangeaceae				X			Nevling, 1964
Melastomataceae				X			Schulman & Hyvönen, 2003
Schlegeliaceae				X			Acevedo-Rodríguez, 2005
Malvaceae						X	Croat, 1978

thorough review of botanical perspectives on handedness terminology up to the early 1970s.

We present here an exhaustive survey of a local climber flora in which handedness of apically twining species is recorded. In contrast to the globally oriented work of Edwards et al. (2007) in which they traversed a trail, counting the first 17 to 121 climbing stems (average of 81) at each of 17 sites (one of which was the Los Amigos site addressed here), we studied a geographically limited climber flora, including as many distinct taxa as possible. This difference between the two studies corrects for the probability of including large numbers of individuals of the same taxon when only the first-encountered, unidentified stems are evaluated, thus decreasing the phylogenetic breadth of the census. Our study addresses climbing plants exclusively from the Neotropics, and thus is also a departure from the excellent compendium of Ornduff (2004) in which plants observed were largely under cultivation in botanical gardens and in which the species observed were predominantly from Africa, Asia, and Australia.

Using our survey, we tested the hypothesis that distinct taxa within a flora are expected to twine

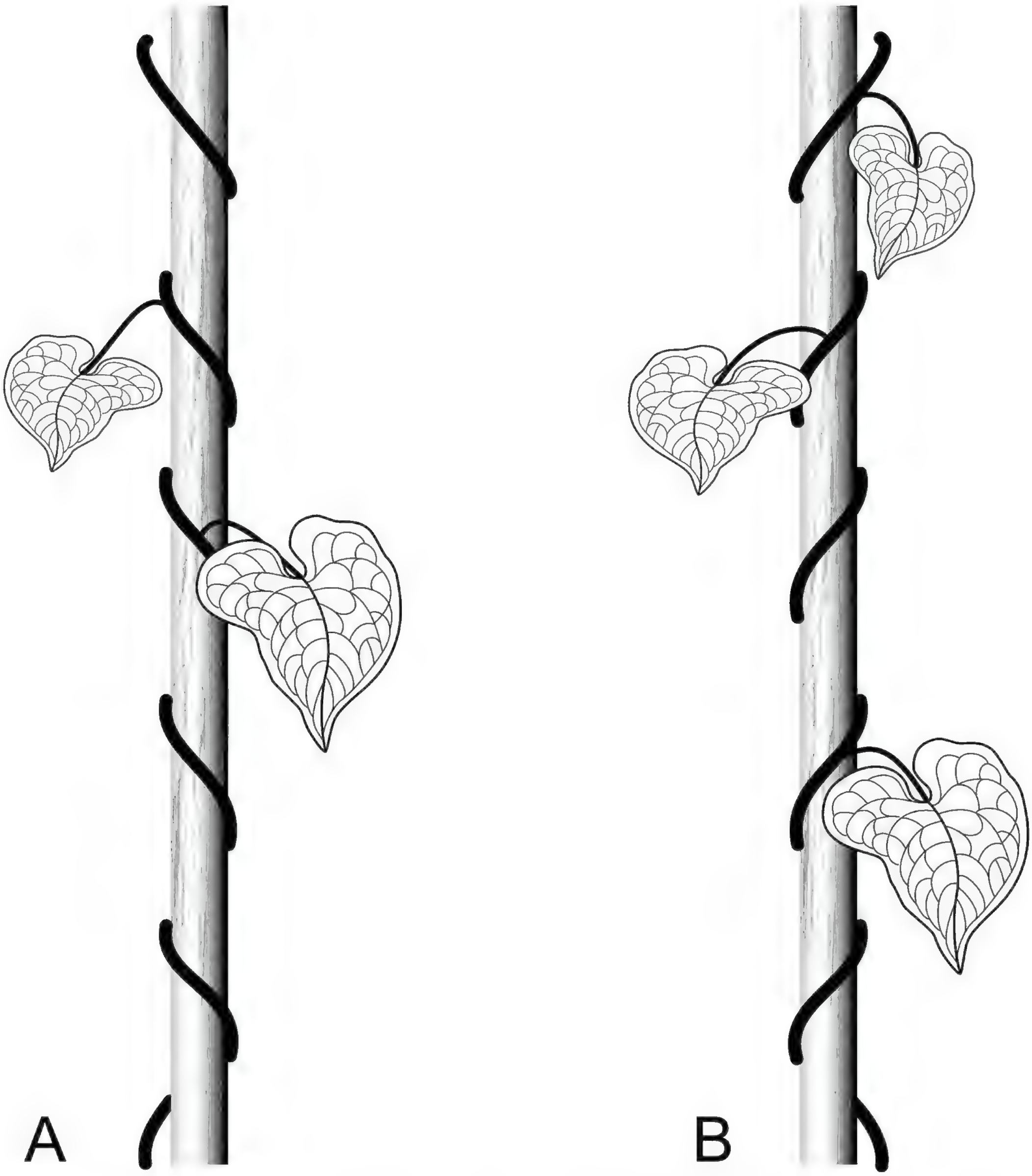

Figure 1. Twining orientation used in this paper. —A. Stem is a sinistral climber, twining from right to left. —B. Stem is a dextral climber, twining from left to right.

Table 2. Explicit definitions and equivalence of twining chirality used in this paper, with notes aiding comparison to other studies.

		Notes
Dextral	Sinistral	Least equivocal terminology.
Right handed	Left handed	Synonyms for dextral and sinistral.
Clockwise	Counterclockwise	If used, this must specify observation perspective as from base of plant; if viewed from above these terms will be reversed; our observation points were from the base of the plant.
Positive	Negative	Designation by Baillaud (1962), whose justification for a new term was that the historical origin of dextral and sinistral was confusing.
Moves against the sun	Follows the sun	Darwin (1876); note this is correct only for Northern Hemisphere observations.

predominantly with a dextral chirality (rather than 50% dextral, 50% sinistral). Further, we evaluated the earlier observations that twining chirality (and thus circumnutation) is phylogenetically constrained among angiosperm families that include climbers. Here we propose that if individual censuses (that is, counting every stem in an area) differ from taxa-based censuses in twining chirality patterns, it may suggest that there is an ecological advantage to sinistral twining, despite the predominance of dextral orientation among species. For example, if sinistrally climbing individuals are present in higher proportions than sinistrally climbing taxa, it would suggest that sinistral orientation may be linked to ecological success.

Methods

Our work was carried out in southeastern Peru (Madre de Dios Region) at the Los Amigos Biological Station (12°34′07″S, 70°05′57″W). During a complete census of two 0.5-ha forest plots for climber distribution, diversity, and density, we also made observations on the orientation of climbing in stem-twining species. We also surveyed the margins of 5.2 km of forested trails in the area to record twining chirality. We included up to eight individuals of the same taxon in our tallies. We chose eight as a maximum observation number, based on the probability (1 in 250) of incorrectly coding a taxon as demonstrating a single twining chirality if both dextral and sinistral were present in equal numbers in the population. In reality, most climbing taxa are sufficiently rare in the Los Amigos area, so that we observed most taxa only two to three times. Thus, we maximized phylogenetic diversity and minimized duplicate observations of the same taxon. We excluded from our observations all taxa whose main mechanism of ascent is by tendrils, hooks, or spines (e.g., members of the Sapindaceae, Bignoniaceae, Passifloraceae, Rhamnaceae, etc.), even if their stems weakly twined. We arbitrarily chose to record an individual only when the stem twined at least three times around its support. In evaluating stems for the census, we excluded any individual of a taxon seen within 20 m of the last observation of that same taxon to avoid, as much as possible, censusing the same individual (via cloning) more than once. All individuals were growing in densely shaded terra firme habitats, and all were vigorously growing adults but without evident fruits or flowers, i.e., currently sterile specimens.

Individuals censused were included if we could identify the taxon at least to family. Morphospecies names were used to designate distinct entities for unknown species or genera. Observations were combined into single morphospecies for cases in which we were not confident of the distinctness of the individuals in question. Thus, we estimate that there is more taxonomic diversity represented than we report. Herbarium vouchers were made of species from the 0.5-ha plots, but not from all individuals from trail censuses (see Table 3). Specimens are deposited at Universidad Agraria La Molina in Lima, Peru (MOL), and at the University of Michigan Herbarium (MICH), U.S.A. Based on the first author's experience with climbers of the western Amazon region, we are confident of our placement of the individuals counted into the proper taxonomic group.

Results and Discussion

A total of 145 climbing individuals were recorded for chirality (dextral vs. sinistral), representing 60 distinct taxa (Table 3). We identified 27 individuals only to family, 37 individuals to genus, and 81 to species. The 60 taxa represent 21 families in which the dominant mode of climbing is by stem twining. In 17 of the 21 families, twining chirality was dextral, whereas three families were consistently sinistral and one family included individuals whose stems switched back and forth between sinistral and dextral. At the species level, the pattern is equally clear, with 50 of 60 (83%) taxa circumnutating dextrally. This is congruent with, although lower than, a global average of 92.4% dextral orientation in unidentified stems surveyed by Edwards et al. (2007: 795). Their Los Amigos average was 86.8% based on the site count of 79 unidentified stems.

Our census included a large proportion of the climbing taxa in the area of Los Amigos. In our censuses of two 0.5-ha plots, we encountered ca. 70 and 80 species of lianas in the two plots (stems $\geq$ 1 cm diam.; unpubl. data). Of those species, about 35 and 40 species, respectively, were stem twiners, while the remainder was a mix of tendrillate, hooking, root-climbing, spiny, and scrambling lianas. Thus, we believe that our observations of 60 taxa from Los Amigos trails, combined with observations made on the two 0.5-ha plots, include most of the stem-twining taxa in the area of the Los Amigos Biological Station. The data are thus a taxon-based (vs. stem-based) census of the twining chirality of climbers at Los Amigos.

Taxa that only circumnutated sinistrally included all specimens of the Dioscoreaceae, Piperaceae, and Asteraceae, and only taxa in these families (Table 3). Although our survey included only one or two species

Table 3. Summary of chirality in 60 twining taxa observed at the Los Amigos Biological Station, Peru. No individuals were censused within 20 m of another individual of the same taxon to avoid censusing clonal individuals. One to eight individuals were censused per taxon; total number of individuals censused was 145.

Family	Genus	Species or morphospecies	Burnham collection number[1]	No. of individuals observed	Twining chirality[2]
Acanthaceae	*Mendoncia* Vell. ex Vand.	sp. indet. 1	RJB 3433	3	D
Acanthaceae	*Mendoncia*	*sericea* Leonard	RJB 3669	3	D
Acanthaceae	*Mendoncia*	sp. indet. 3	RJB 3713, RJB 3596	3	D
Apocynaceae	*Forsteronia* G. Mey.	*amblybasis* S. F. Blake	RJB 3611	7	D
Apocynaceae	*Forsteronia*	*acouci* (Aubl.) A. DC.	RJB 3568, 3661	2	D
Apocynaceae	*Odontadenia* Benth.	*puncticulosa* (Rich.) Pulle	RJB 3491	1	D
Apocynaceae	*Odontadenia*	*verrucosa* (Willd. ex Roem. & Schult.) K. Schum. ex Markgr.	RJB 3584	1	D
Apocynaceae	*Gonolobus* Michx.	sp. indet. 1	RJB 3557	3	D
Apocynaceae	genus indet. 1	sp. indet. 1	–	2	D
Apocynaceae	genus indet. 2	sp. indet. 1	–	1	D
Aristolochiaceae	*Aristolochia* L.	sp. indet. 1	–	1	D
Aristolochiaceae	*Aristolochia*	sp. indet. 2	–	1	D
Aristolochiaceae	*Aristolochia*	*dalyi* F. González	RJB 3690, 3712	2	D
Asteraceae	*Mikania* Willd.	*guaco* Humb. & Bonpl.	RJB 3499	8	S
Asteraceae	*Mikania*	sp. indet. 1	–	1	S
Combretaceae	*Combretum* Loefl.	*laxum* Jacq.	RJB 3542, 3616	7	D
Combretaceae	*Combretum*	*assimile* Eichler	RJB 3664	1	D
Combretaceae	genus indet. 1	sp. indet. 1	RJB 3587	1	D
Connaraceae	*Pseudoconnarus* Radlk.	*macrophyllus* (Poepp.) Radlk.	RJB 3561	1	D
Convolvulaceae	*Ipomoea* L.	sp. indet. 1	–	5	D
Convolvulaceae	*Maripa* Aubl.	sp. indet. 1	RJB 3670	1	D
Convolvulaceae	*Dicranostyles* Benth.	sp. indet. 1	RJB 3586	1	D
Dichapetalaceae	*Dichapetalum* Thouars	sp. indet. 1	RJB 3738	2	D
Dilleniaceae	genus unknown	sp. indet. 1	RJB 3490, 3551	2	S, D
Dilleniaceae	genus unknown	sp. indet. 2	RJB 3488	4	S, D
Dilleniaceae	genus unknown	sp. indet. 3	RJB 3583	4	S, D
Dilleniaceae	genus unknown	sp. indet. 4	RJB 3520	2	S, D
Dilleniaceae	genus unknown	sp. indet. 5	RJB 3688	2	S, D
Dioscoreaceae	*Dioscorea* L.	sp. indet. 1	–	2	S
Euphorbiaceae	*Plukenetia* L.	*brachybotrya* Müll. Arg.	RJB 3684	2	D
Fabaceae	*Deguelia* Aubl.	sp. indet. 1	RJB 3654	3	D
Fabaceae	genus unknown	sp. indet. 1	–	3	D
Fabaceae	genus unknown	sp. indet. 2	RJB 3639	1	D
Fabaceae	genus unknown	sp. indet. 3	–	1	D
Hernandiaceae	*Sparattanthelium* Mart.	*tarapotanum* Meisn.	RJB 3706, 3721	1	D
Malpighiaceae	*Mezia* Schwacke ex Nied.	sp. indet. 1	RJB 3426	4	D
Malpighiaceae	genus unknown	sp. indet. 2	–	3	D
Malpighiaceae	genus unknown	sp. indet. 3	–	1	D
Malpighiaceae	*Banisteriopsis* C. B. Rob.	*muricata* (Cav.) Cuatrec.	RJB 3437	1	D
Malpighiaceae	*Mascagnia* (Bertero ex DC.) Colla	*dissimilis* C. V. Morton & Moldenke	RJB 3521	2	D
Malpighiaceae	*Hiraea* Jacq.	*fagifolia* (DC.) A. Juss.	RJB 3702	4	D
Malpighiaceae	*Hiraea*	sp. indet. 2	–	1	D
Malpighiaceae	*Tetrapterys* Cav.	sp. indet. 1	RJB 3566	1	D
Malvaceae	*Byttneria* Loefl.	*benensis* Britton	RJB 3715	2	D
Menispermaceae	*Sciadotenia* Miers	*toxifera* Krukoff & A. C. Sm.	RJB 3710, 3567	2	D
Menispermaceae	*Abuta* Aubl.	*rufescens* Aubl.	–	2	D
Menispermaceae	*Anomospermum* Miers	*grandifolium* Eichler	–	4	D
Menispermaceae	*Anomospermum*	*chloranthum* Diels	RJB 3692	4	D

Table 3. Continued.

Family	Genus	Species or morphospecies	Burnham collection number[1]	No. of individuals observed	Twining chirality[2]
Menispermaceae	*Cissampelos* L.	*pareira* L.	RJB 3478	2	D
Menispermaceae	*Disciphania* Eichler	sp. indet. 1	RJB 3461	3	D
Menispermaceae	*Telitoxicum* Moldenke	*minutiflorum* (Diels) Moldenke	RJB 3735	1	D
Olacaceae	*Heisteria* Jacq.	*scandens* Ducke	RJB 3647	2	D
Piperaceae	*Manekia* Trel.	*sydowii* (Trel.) T. Arias, Callejas & Bornst.	RJB 3568	3	S
Piperaceae	*Piper* L.	sp. indet. 1	–	2	S
Polygonaceae	*Coccoloba* P. Browne	*excelsa* Benth.	RJB 3425	3	D
Polygonaceae	*Coccoloba*	*marginata* Benth.	RJB 3435	5	D
Polygonaceae	*Coccoloba*	*parimensis* Benth.	RJB 3588	2	D
Rubiaceae	*Manettia* Mutis ex L.	*cordifolia* Mart.	–	1	D
Verbenaceae	*Petrea* L.	*blanchetiana* Schauer	RJB 3585	1	D
Verbenaceae	*Petrea*	*maynensis* Huber	RJB 3608	4	D

[1] Collection numbers provided only for collected specimens; vouchered specimens are deposited at MOL and MICH.
[2] D = dextral, S = sinistral.

in each of these families (16 of the 145 individuals, 11%), our results on the frequency of sinistral circumnutation are supported by our observations from other regions of the Amazon Basin as well as in the temperate zone of North America (R. J. Burnham, unpubl. data). Literature documentation (Darwin, 1876; Baillaud, 1962; Ornduff, 2004) of temperate and tropical genera exhibiting sinistral twining also includes *Humulus* L. spp. (Cannabaceae); *Fallopia* Adans., *Muehlenbeckia* Meisn., and *Polygonum* L. spp. (Polygonaceae); *Scyphanthus elegans* Sweet (Loasaceae); various members of the Rubiaceae; all members of the Illiciaceae that have been observed; and *Clerodendrum* L. spp. (Lamiaceae). Possibly closely related to *Clerodendrum* are members of *Petrea* L. (Verbenaceae), which was observed to twine dextrally at Los Amigos.

The Dilleniaceae deserves special mention because of its curious behavior. In almost all individuals and taxa observed, stems circumnutated in one direction, and after two to three revolutions they changed direction and circumnutated in the opposite direction for two to three revolutions. We observed two sequential changes in twining direction in at least 10 of the 14 individuals of Dilleniaceae that we included in our observations. Darwin also noted this curious behavior in a single dilleniaceous individual of *Hibbertia* Andrews (Darwin, 1876: 26, 36). Darwin also observed that the Loasaceae species *Loasa aurantiaca* Urb. & Gilg and *Scyphanthus elegans* exhibit chirality changes in individual stems. Here we call this phenomenon ambidextrous twining when encountered within a single species. The largely temperate species *Solanum dulcamara* L. is another example of ambidextrous twining (Dufour, 1902; Baillaud, 1962; Ornduff, 2004), but it also employs the scrambling mechanism, which assists in supporting the individuals as they climb. These are the only species we are aware of with a change in chirality during ontogeny. We have only observed this occurring in members of the Dilleniaceae, and have never seen any of the dextrally circumnutating species showing evidence of reversing direction during growth.

Chirality of twiners is phylogenetically correlated, with almost every family that includes stem-twining taxa showing consistently dextral circumnutation, and those that are sinistral also showing consistency within the family. Our census included eight families represented by a single taxon (12 individuals) and 13 families represented by two to seven taxa. Within each family, the taxa show consistent chirality. This suggests that climbing orientation may be nearly universal within a family. The interesting deviations from the typically dextral chirality of species at Los Amigos are not phylogenetically closely related. Piperaceae is a member of the Magnoliid basal angiosperm clade, Dioscoreaceae is a monocot, and Asteraceae is a member of the euasterid campanuliid clade (Angiosperm Phylogeny Group III, 2009). Dilleniaceae (the family in which inconsistent orientation was noted) has been placed as a sister to Caryophyllales and is a basal core eudicot, again not particularly close to any of the other sinistral families. There are some intriguing reports of families in which both dextral and sinistral chirality can be found: Baillaud (1962) reported *Anchietea* A. St.-Hil. as dextral and *Corynostylis* Mart. & Zucc. as sinistral,

both of which are woody climbing members of the Violaceae. The same author reported species of *Dioscorea* L. twining dextrally or sinistrally, or able to change direction during ontogeny. These reports are exciting, although they stem from relatively few observations. Still, these exceptions may provide a fertile avenue for investigating the basis for chiral asymmetry among flowering plants.

Our data represent a phylogenetically broad and floristically complete perspective on previous observations on the predominance of twining chirality. It documents the phylogenetic distribution of chirality among twiners in a single Amazonian forest and underscores the gap in our understanding of the predominance of dextral orientation among angiosperm twiners. The stem-twining habit has clearly evolved multiple times in different angiosperm lineages, as evidenced by the mix of ancestral habits (shrub, tree, climber) found among angiosperm clades (Angiosperm Phylogeny Group III, 2009). A developmentally based argument for the importance of dextral chirality in climbers must also include a perspective on the chirality in organs of nonclimbers (e.g., flowers, buds, wood) that would be consistent with such an explanation. The literature indicates no similar chirality predominance in other plant organs (Gardner, 1990; Endress, 2001; Welch, 2002). Why the orientation of stem-twiners should be so consistently dextral has not yet been adequately answered by recent research on the physical properties of circumnutation and support of vines (Silk & Hubbard, 1991; Silk & Holbrook, 2005; Goriely & Neukirch, 2006; Bowling & Vaughn, 2009).

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DEVELOPMENTAL ANATOMY AND MORPHOLOGY OF THE FLOWERS AND FRUITS OF SPECIES FROM *GALIUM* AND *RELBUNIUM* (RUBIEAE, RUBIACEAE)[1]

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Abstract

The circumscription of genera within the family Rubiaceae is by no means a precise endeavor at the current time. For example, the genus *Relbunium* (Endl.) Hook. f. is currently included as a section of *Galium* L., sensu Dempster, although this placement does not have unanimous support among specialists. To clarify these uncertainties, this study examined whether *Relbunium* is an autonomous genus or a section of *Galium* by analyzing the morphology and development of flowers and fruits of the following species: *G. latoramosum* Clos, *G. uruguayense* Bacigalupo, *R. equisetoides* (Cham. & Schltdl.) Ehrend., *R. gracillimum* Ehrend., *R. hirtum* (Lam.) K. Schum., *R. humile* (Cham. & Schltdl.) K. Schum., *R. humilioides* M. L. Porto & Ehrend., *R. hypocarpium* (L.) Hemsl., *R. longipedunculatum* Mariath & Ehrend., *R. mazocarpum* Greenm., *R. megapotamicum* (Spreng.) Ehrend., *R. nigro-ramosum* Ehrend., *R. ostenianum* Standl., *R. richardianum* (Gillies ex Hook. & Arn.) Hicken, and *R. valantioides* (Cham. & Schltdl.) K. Schum. This morphological data set and analysis were then used to construct a cladogram, which indicates that *Galium* is a sister group to *Relbunium* and further characterizes *Relbunium* as a monophyletic clade that should be considered an autonomous genus.

Key words: Evolution, *Galium*, pericarp, phylogeny, *Relbunium*, Rubiaceae, seed, seed coat.

The family Rubiaceae has a cosmopolitan distribution and is frequently encountered in tropical and subtropical regions (Dillenburg, 1978). Members of this family can be easily recognized by the presence of an inferior ovary, opposite and decussate leaves with interpetiolar stipules with colleters, a nuclear endosperm, the widespread occurrence of alkaloids, and the absence of an internal phloem (Bremer, 1992, 1996). Despite the well-defined morphological characteristics that distinguish Rubiaceae from other plant families, intrafamily delimitations are complex. Moreover, the species of Rubiaceae are biologically and morphologically quite diverse and have distinct habits and reproductive characteristics (Bremer et al., 1995).

The parallel evolution of similar morphological characters within otherwise distinct groups, together with a scarcity of morphological and phylogenetic studies (Bremer & Jansen, 1991), have led to the lack of taxonomic consensus. This confusion relates to subfamilies and tribes, but there are also ongoing discussions concerning the delimitation of the component genera and species, such as the *Hedyotis* L.–*Oldenlandia* L. complex in the genus *Psychotria* L. (Bremer & Jansen, 1991) and the genera *Galium* L. and *Relbunium* (Endl.) Hook. f. (Dempster, 1981, 1982, 1990).

The first taxonomic studies of the genus *Relbunium* were published in 1839 and included 20 species for *Rubia* L. sect. *Involucratae* DC. (de Candolle, 1839), which was characterized by the presence of an involucre below the sessile flower. The name *Relbunium* was first proposed by Endlicher (1839) as a section within the genus *Galium*. Later, in 1873, a generic rank was recognized by Bentham and Hooker. Schumann (1889) cited 22 species for the genus *Relbunium* and established the appropriate binomials for the first time. In 1955, Ehrendorfer published a detailed description of *Relbunium*, recognizing 30 species distributed among sections,

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subsections, and series. According to this author, the delimitations of the genera *Relbunium* and *Rubia* principally result from their respective geographic distributions, as well as differences in their growth forms, corolla, and fruit. Ehrendorfer (1955) suggested that the closer morphological relationships between the American species of *Galium* and *Relbunium* indicated that *Relbunium* originated from *Galium* in the New World. Dempster (1978) viewed *Relbunium* as a clearly monophyletic group, even though its species are often confused with those of *Galium*. This author further affirmed that the species of *Relbunium* are easily distinguished when flowering or fruiting, observing that involucres are absent in *Galium*, whereas species in *Relbunium* exhibit four involucral bracts subtending each flower. However, according to Dempster (1978), numerous other vegetative morphological characteristics are common to both genera, supporting *Relbunium* as a section of *Galium*, as first proposed by Endlicher (1839).

In 1982, Dempster mentioned that the genus *Relbunium* should be limited to taxa with solitary and essentially sessile flowers with involucres. Based on this observation, the author transferred all of the species without these characteristics into the genus *Galium*. In her last work with South American *Galium*, Dempster (1990) returned to the proposals of Endlicher (1839) and defined *Relbunium* as a section of *Galium*.

Plastid DNA sequence analyses of species of Rubieae (Natali et al., 1996) included *Relbunium* as *R. hypocarpium* (L.) Hemsl., but did not further address taxonomic issues. Bremer and Manen (2000) included 14 genera in their classification for the Rubieae and treated *Relbunium* separately from *Galium*.

Galium comprises approximately 400 species (Judd et al., 1999), of which ca. 90 are found in the Neotropics (Andersson, 1992). The genus *Relbunium* comprises ca. 35 Neotropical species that are distributed from the southwestern United States (Porto et al., 1977). These species preferentially grow in open fields and forest borders in subtropical regions. Approximately 22 species are known for the southern regions of South America, including southern Brazil, Uruguay, and Argentina (Chamisso & Schlechtendal, 1828; de Candolle, 1839; Schumann, 1891; Ehrendorfer, 1955; Smith & Down, 1956; Rambo, 1962; Porto et al., 1977). Approximately 39% of *Relbunium* species, representing over half of the described South American species of *Relbunium*, are included in the morphological survey herein.

Fruits and seeds are always important in taxonomic classifications of Rubiaceae, as can be seen in Schumann (1891), Bremekamp (1966), and Robbrecht (1988). In addition to characterizing subfamilies and tribes, fruits and seeds have been used to distinguish genera, as in the case of *Appunia* Hook. f. and *Morinda* L. (Hayden & Dwyer, 1969). These infrafamilial morphological variations indicate a diversity of adaptations, especially in terms of seed dispersal (Bremer & Eriksson, 1992). Even though previous studies have variously treated *Galium* and *Relbunium*, there has been insufficient work focusing on their taxonomy that could integrate the anatomical, morphological, ecological, and molecular evidences. Few works describe the morphology and anatomy of the flowers, fruits, and seeds of these taxa in terms of their phylogenetic significance. According to Corner (1976), there is a need for extensive ontogenetic investigations of the pericarp, integument thickness, and the structure of the seed coat at the genus and species levels in the Rubiaceae. Consequently, the present study examines the structure and development of the flowers, fruits, and seeds within exemplar species of *Galium* and *Relbunium* to elucidate additional taxonomic characteristics toward the delimitation and relative ranks of these two groups/taxa.

Materials and Methods

We examined 13 species of *Relbunium* (sensu Ehrendorfer, 1955, modified by Porto et al., 1977) and two species of *Galium*, as well as two other species within the Rubioideae as outgroups. For examination of species within *Relbunium*, exemplars were chosen to represent all sections and subsections recognized by Ehrendorfer (1955). All botanical material was deposited in the herbarium of the Rio de Janeiro Botanical Garden (RB), as shown in Table 1.

All material destined for optical microscopic analysis was fixed immediately after collection in 2.5% glutaraldehyde in 0.1 M sodium phosphate buffer, pH 7.2 (Gabriel, 1982), dehydrated in an ethanol series, embedded in Leica HistoResin (2-hydroxyethyl-metracrylate) (Nussloch, Germany), sectioned in a Shandon Hypercut microtome (Runcorn, Cheshire, U.K.) at 2–4 μm, and then stained with toluidine blue O 0.05% (O'Brien & McCully, 1981). Observations (in bright field) were made using an Olympus BX50 optical microscope (Center Valley, Pennsylvania, U.S.A.) equipped with a CoolSnap-pro digital camera (Houston, Texas, U.S.A.). Histochemical analyses were performed using Sudan III to

Table 1. Specimens examined. The vouchers are deposited at Rio de Janeiro Botanical Garden Herbarium (RB).

Taxa	Collection data
Galium latoramosum Clos	Brazil. Rio Grande do Sul: Ijuí, 24 Oct. 1984, *R. Bueno s.n.* (RB 444232); 30 Aug. 1904, *A. Bornmuller 132* (GH). Santa Catarina: Nova Teutônia, 3 Sep. 1944, *F. Plaumann 120* (RB).
G. uruguayense Bacigalupo	Brazil. Rio Grande do Sul: Caçapava do Sul, 3 May 2002, *K. De Toni s.n.* (RB 444168); Cristal do Sul, 20 Aug. 2001, *K. De Toni s.n.* (RB 444206); Guaíba, 11 Jan. 2003, *K. De Toni s.n.* (RB 444228).
Relbunium equisetoides (Cham. & Schltdl.) Ehrend.	Brazil. Rio Grande do Sul: Guaíba, 20 Feb. 2003, *N. I. Matzembacher s.n.* (RB 444212), *K. De Toni et al. s.n.* (RB 444210).
R. gracillimum Ehrend.	Brazil. Rio de Janeiro: Angra dos Reis, 22 Sep. 2004, *M. G. Bovini et al. 2460* (RB); Itatiaia, Mar. 2003, *K. De Toni et al. s.n.* (RB 4444211).
R. hirtum (Lam.) K. Schum.	Brazil. Rio Grande do Sul: Lavras do Sul, 4 May 2002, *K. De Toni et al. s.n.* (RB 444164).
R. humile (Cham. & Schltdl.) K. Schum.	Brazil. Rio Grande do Sul: Cambará do Sul, 9 Mar. 2002, *K. De Toni et al. s.n.* (RB 444192); 7 Apr. 2002, *K. De Toni et al. s.n.* (RB 444173); 26 Dec. 2002, *K. De Toni et al. s.n.* (RB 444216); Guaíba, 11 Jan. 2003, *K. De Toni et al. s.n.* (RB 444227); Jaquirana, 6 Apr. 2002, *K. De Toni et al. s.n.* (RB 444177); Maquiné, 26 Dec. 2002, *K. De Toni et al. s.n.* (RB 444217); Porto Alegre, 4 Oct. 2001, *K. De Toni et al. s.n.* (RB 444200); Tainhas, 29 Nov. 2001, *K. De Toni et al. s.n.* (RB 444197).
R. humilioides M. L. Porto & Ehrend.	Brazil. Rio Grande do Sul: Cambará do Sul, 9 Mar. 2002, *K. De Toni et al. s.n.* (RB 444188); 7 Apr. 2002, *K. De Toni et al. s.n.* (RB 444229).
R. hypocarpium (L.) Hemsl.	Brazil. Rio Grande do Sul: Barra do Ouro, 26 Dec. 2002, *K. De Toni et al. s.n.* (RB 444213); Caçapava do Sul, 3 June 2002, *K. De Toni et al. s.n.* (RB 444165, 444166); Cambará do Sul, 9 Mar. 2002, *K. De Toni et al. s.n.* (RB 444171); 29 Mar. 2002, *K. De Toni et al. s.n.* (RB 444178); 7 Apr. 2002, *K. De Toni et al. s.n.* (RB 444180); Porto Alegre, 6 Aug. 2001, *K. De Toni et al. s.n.* (RB 444207); Santo Antônio da Patrulha, 22 Aug. 2001, *K. De Toni et al. s.n.* (RB 444203); São José dos Ausentes, 10 Mar. 2002, *K. De Toni et al. s.n.* (RB 444184, 444185).
R. longipedunculatum Mariath & Ehrend.	Brazil. Rio Grande do Sul: Cambará do Sul, 9 Mar. 2002, *K. De Toni et al. s.n.* (RB 44189); 29 Mar. 2002, *K. De Toni et al. s.n.* (RB 444179); 7 Apr. 2002, *K. De Toni et al. s.n.* (RB 444170); 26 Dec. 2002, *K. De Toni et al. s.n.* (RB 444215); 5 Jan. 2004, *K. De Toni et al. s.n.* (RB 444160); Jaquirana, 6 Apr. 2002, *K. De Toni et al. s.n.* (RB 444175).
R. mazocarpum Greenm.	Brazil. Rio Grande do Sul: Cambará do Sul, 29 Mar. 2002, *K. De Toni et al. s.n.* (RB 444181).
R. megapotamicum (Spreng.) Ehrend.	Brazil. Rio Grande do Sul: Tainhas, 29 Mar. 2002, *K. De Toni et al. s.n.* (RB 444182); 29 Nov. 2002, *K. De Toni et al. s.n.* (RB 444196).
R. nigro-ramosum Ehrend.	Brazil. Rio Grande do Sul: Burro Novo, 6 Sep. 2004, *K. De Toni et al. s.n.* (RB 444230); Caçapava do Sul, 3 June 2002, *K. De Toni et al. s.n.* (RB 444167); Cambará do Sul, 9 Mar. 2002, *K. De Toni et al. s.n.* (RB 444187); 7 Apr. 2002, *K. De Toni et al. s.n.* (RB 444172); Jaquirana, 6 Apr. 2002, *K. De Toni et al. s.n.* (RB 444176); São Francisco de Paula, 29 Nov. 2001, *K. De Toni et al. s.n.* (RB 444198); 26 Dec. 2002, *K. De Toni et al. s.n.* (RB 444158); São José dos Ausentes, 10 Mar. 2002, *K. De Toni et al. s.n.* (RB 444186); Tainhas, 29 Nov. 2001, *K. De Toni et al. s.n.* (RB 444194).
R. ostenianum Standl.	Brazil. Rio Grande do Sul: Caçapava do Sul, 4 June 2002, *K. De Toni et al. s.n.* (RB 444224).
R. richardianum (Gillies ex Hook. & Arn.) Hicken	Brazil. Rio Grande do Sul: Cristal do Sul, 20 Aug. 2001, *K. De Toni et al. s.n.* (RB 444205); Lavras do Sul, 4 June 2002, *K. De Toni et al. s.n.* (RB 444163); Porto Alegre, 2 Aug. 2001, *K. De Toni et al. s.n.* (RB 444221); 16 Aug. 2001, *K. De Toni et al. s.n.* (RB 444222); Santo Antônio da Patrulha, 22 Aug. 2001, *K. De Toni et al. s.n.* (RB 444203); São Francisco de Paula, 9 Mar. 2002, *K. De Toni et al. s.n.* (RB 444193).
R. valantioides (Cham. & Schltdl.) K. Schum.	Brazil. Rio Grande do Sul: Santo Antônio da Patrulha, 22 Aug. 2001, *K. De Toni et al. s.n.* (RB 444195).
Borreria verticillata (L.) G. Mey.	Brazil. Rio Grande do Sul: Porto Alegre, *K. De Toni et al. 05* (RB).
Psychotria carthagenensis Jacq.	Brazil. Rio Grande do Sul: Porto Alegre, *K. De Toni et al. 06* (RB).

detect total lipids (O'Brien & McCully, 1981) and periodic acid Schiff (PAS) reaction to detect soluble polysaccharides (O'Brien & McCully, 1981).

Samples for SEM were fixed and then prepared according to the protocol described by Gersterberger and Leins (1978). Samples were dehydrated and prepared using a CPD 030 critical point dryer (Baltec, Schalksmühle, Germany), metal-coated using a Balzers SCD 050 sputtering system (Munich, Germany), and observed with a JEOL 5800 or DSEM 962 Zeiss scanning electron microscope (Oberkochen, Germany) with digital image acquisition.

Using morphological data (Appendix 1), a numerical matrix with 55 characters was constructed (Appendix 2). Parsimony analyses were performed using PAUP version 4.0b10 software (Swofford, 2002). The character states were treated as unordered, and the trees calculated using the neighbor-joining parsimony method. The confidence in the groups formed in these trees was verified using bootstrap and jackknife resampling tests with 1000 replicates for each analysis. The trees obtained were subsequently plotted and evaluated using the MacClade 4.0 software package (Maddison & Maddison, 2000).

Results

Flowers

All the species had solitary flowers (cf. Appendix 2, character 2, state 0), except for *Galium latoramosum* Clos, *Relbunium equisetoides* (Cham. & Schltdl.) Ehrend., *R. richardianum* (Gillies ex Hook. & Arn.) Hicken, and the two outgroup taxa, which had compound dichasium, simple dichasium, and monochasium inflorescences.

All species of *Relbunium* examined had two, three, or four bracts. Species with four bracts had either two identical or unequal pairs (Fig. 1A–H); when unequal, there was one larger and one smaller pair (Fig. 1I, J). The most species have identical bracts (see Appendix 2, character 9, state 0); only two species present unequal pairs of bracts (Appendix 2, character 9, state 1); and three of them had only two bracts (Appendix 2, character 8, state 0; Fig. 1K–M), although a third bract was often observed in *R. ostenianum* Standl. (Appendix 2, character 8, state 1). Flowers generally had short peduncles (between 1 and 6 mm long) for 11 of the sampled species in *Galium* and *Relbunium* (cf. Appendix 2). Two species, *R. gracillimum* Ehrend. and *R. hypocarpium* (L.) Hemsl., demonstrated longer peduncles, to 15 mm. *Relbunium hirtum* (Lam.) K. Schum. and *R. ostenianum* had peduncles less than 1 mm long, and these flowers were considered sessile. Flowers were sessile in *R. equisetoides* and *R. richardianum*, while flowers of *G. latoramosum* had pedicels to 4 mm. Also, all of the species observed had bisporic flowers; *G. latoramosum*, however, had pistillate and staminate flowers on individual plants, which characterize monosporic flowers.

In terms of the floral whorls, seven species do not present unicellular trichomes on the abaxial face of the corolla (Appendix 2, character 17, state 0; Figs. 1A, E–G, I, J, N, 2A); four species present sparse trichomes on the abaxial face (Appendix 2, character 17, state 2; Figs. 1B, C, M, O, 2B, C); and also in four species unicellular trichomes were only observed along the corolla margins (Appendix 2, character 17, state 1; Figs. 1D, H, K, L, 2D). In addition to trichomes, idioblasts were observed on the abaxial faces of *Relbunium gracillimum* and *R. hypocarpium* (Fig. 2A; Appendix 2, character 22). These idioblasts were concentrated on the distal mid-third of the petals and were rectangular in shape, with dense cytoplasm and a distinct nucleus. Trichomes on the adaxial face were glandular and unicellular, situated near the margins and the central portion of the petals and, invariably, over the vascular bundles (Fig. 2E), or dispersed, as in *Galium uruguayense* Bacigalupo (Fig. 2B). These glandular trichomes were clavate (Fig. 2F, G), and a cuticle with randomly oriented low-ridge saliences (Fig. 2F) was present. During their early development, these trichomes have a large vacuole in their apical portions and a prominent nucleus. In later development, the large vacuole divides into many smaller ones (Fig. 2G). Histochemical tests indicated the presence of lipids and polysaccharides in the cytoplasm of these glandular trichomes.

The androecium is composed of four stamens with dorsifixed anthers, all of them tetrasporangiate (Fig. 2H), situated alternate to the petals and partially attached to them (Fig. 1A, C–O). At dehiscence, the anther walls reduce to only the epidermis and the endothecium (Fig. 2I). The endothecium had elongated cells and demonstrated unequal thickening of the lignified cell walls (Fig. 2I–K). These unequal thickenings appear as bands over the anticlinal walls (Fig. 2J) and as star-shaped (frontal view) over the internal periclinal walls (Fig. 2K). At anther dehiscence, pollen grains are bicellular or tricellular, with isopolar symmetry, forming pentacolpate or hexacolpate prolate spheroids or subprolate spheroids (Fig. 2L).

The gynoecium in *Relbunium* has a bicarpellate, bilocular inferior ovary, with one ovule per locule (Fig. 3A, B); however, tricarpellate ovaries were occasionally seen in *R. ostenianum* (Fig. 3C). The

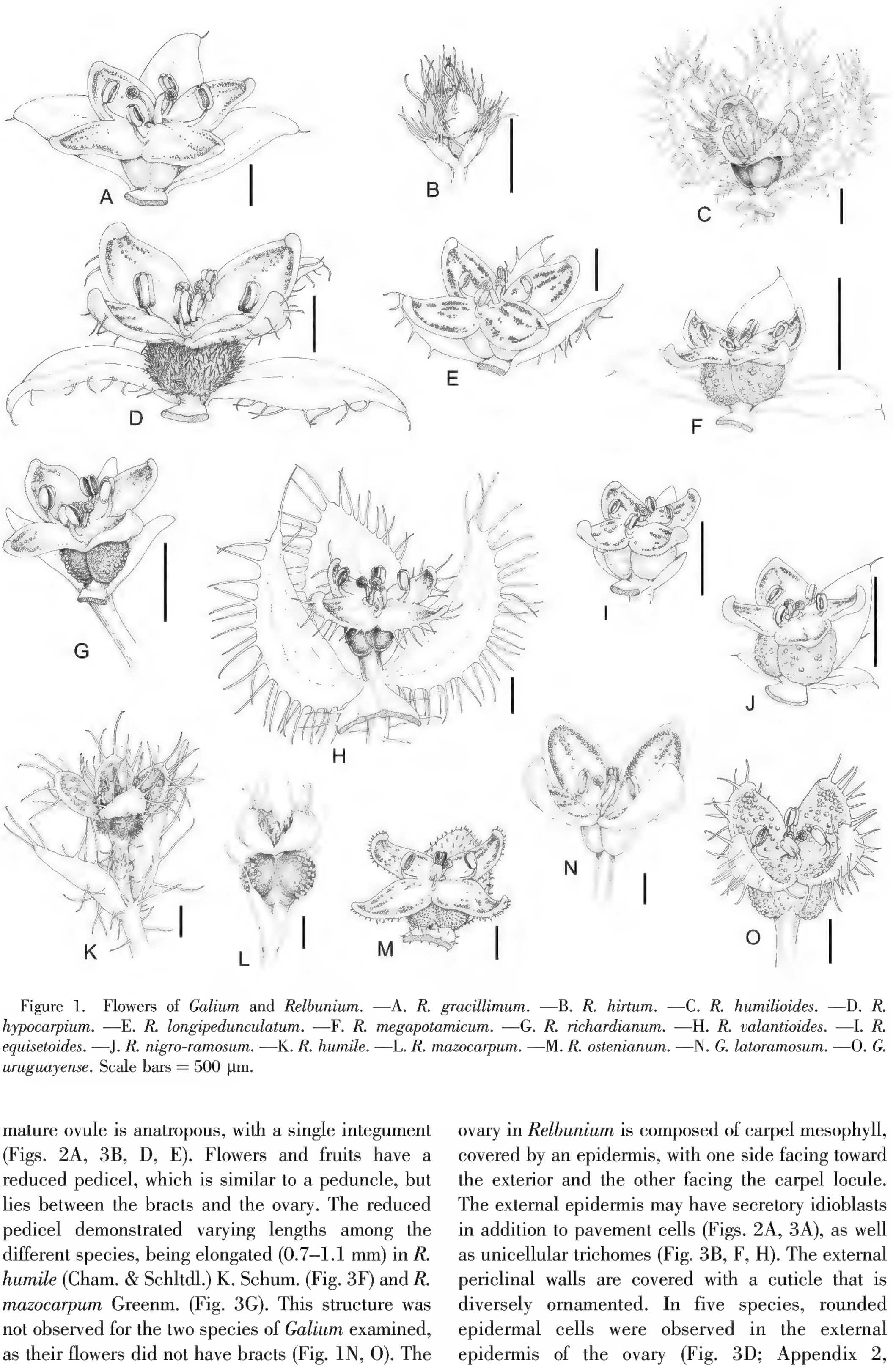

Figure 1. Flowers of *Galium* and *Relbunium*. —A. *R. gracillimum*. —B. *R. hirtum*. —C. *R. humilioides*. —D. *R. hypocarpium*. —E. *R. longipedunculatum*. —F. *R. megapotamicum*. —G. *R. richardianum*. —H. *R. valantioides*. —I. *R. equisetoides*. —J. *R. nigro-ramosum*. —K. *R. humile*. —L. *R. mazocarpum*. —M. *R. ostenianum*. —N. *G. latoramosum*. —O. *G. uruguayense*. Scale bars = 500 μm.

mature ovule is anatropous, with a single integument (Figs. 2A, 3B, D, E). Flowers and fruits have a reduced pedicel, which is similar to a peduncle, but lies between the bracts and the ovary. The reduced pedicel demonstrated varying lengths among the different species, being elongated (0.7–1.1 mm) in *R. humile* (Cham. & Schltdl.) K. Schum. (Fig. 3F) and *R. mazocarpum* Greenm. (Fig. 3G). This structure was not observed for the two species of *Galium* examined, as their flowers did not have bracts (Fig. 1N, O). The ovary in *Relbunium* is composed of carpel mesophyll, covered by an epidermis, with one side facing toward the exterior and the other facing the carpel locule. The external epidermis may have secretory idioblasts in addition to pavement cells (Figs. 2A, 3A), as well as unicellular trichomes (Fig. 3B, F, H). The external periclinal walls are covered with a cuticle that is diversely ornamented. In five species, rounded epidermal cells were observed in the external epidermis of the ovary (Fig. 3D; Appendix 2,

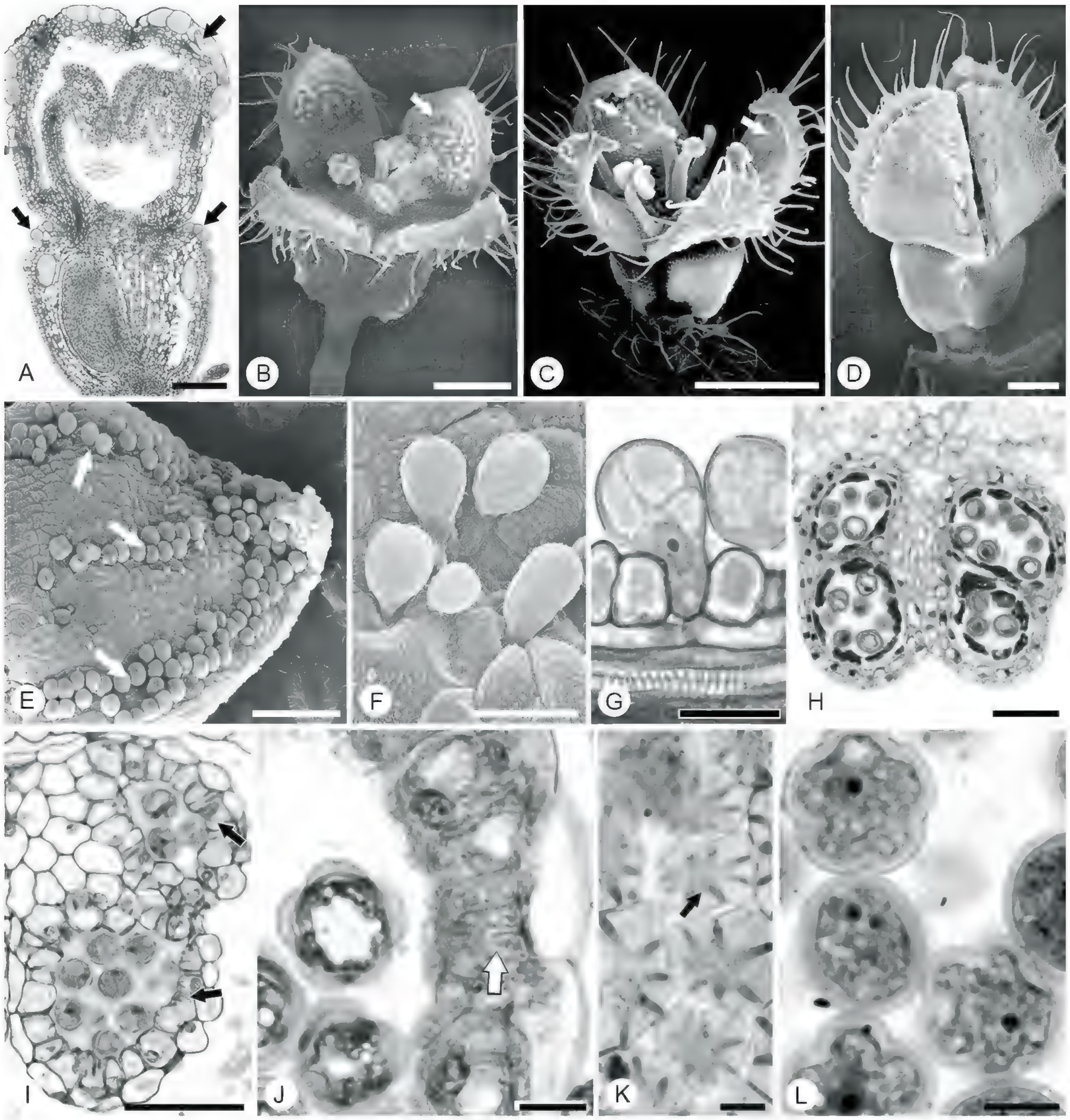

Figure 2. Flowers of *Galium* and *Relbunium*. —A. *R. gracillimum*. Flower bud, longitudinal section; corolla and ovary with idioblasts (arrows). —B. *G. uruguayense*. SEM of flower, glandular trichomes indicated (arrow). —C. *R. humilioides*. SEM of flower, evidencing glandular trichomes (arrows). —D. *R. valantioides*. SEM of flower bud. —E. *G. latoramosum*. SEM of corolla, adaxial view, with glandular trichomes (arrows). —F. *R. richardianum*. SEM of glandular trichomes of corolla (adaxial view). —G. *R. richardianum*. Glandular trichomes of corolla, transverse section (adaxial view). —H. *R. mazocarpum*. Anther tetrasporangiate, transverse section. —I. *R. hirtum*. Anther, transverse section, with endothecium cells (arrows). —J. *R. nigro-ramosum*. Anther details, transverse section, evidencing the endothecium (arrows). —K. *R. hirtum*. Frontal view of endothecium cells, with unequal wall thickness (arrow). —L. *R. hirtum*. Pollen grain detail. Scale bars: F, J–L = 50 μm; G, H, I = 100 μm; B, E = 200 μm; A, C, D = 500 μm.

character 26). In *R. hirtum*, these epidermal cells are secretory, as the cuticle became deformed by the accumulation of secretions between it and the external periclinal wall (Fig. 3E).

The secretory idioblasts of *Galium uruguayense* (Fig. 3I; cf. also Appendix 2, character 30), *Relbunium richardianum*, *R. gracillimum* (Fig. 2A), *R. nigro-ramosum* Ehrend. (Fig. 3A), *R. megapotamicum* (Spreng.) Ehrend. (Fig. 3J), and *R. mazocarpum* were scattered over the external surface of the epidermis, except for the region near the ovary septum (Fig. 3G). In *R. gracillimum* (Fig. 2A), idioblasts were observed only on the superior portion of the ovary, near the corolla. Unicellular trichomes were observed in *R. ostenianum* (Fig. 3B), *R. humile* (Fig. 3F), and *R. hypocarpium* (Fig. 3H).

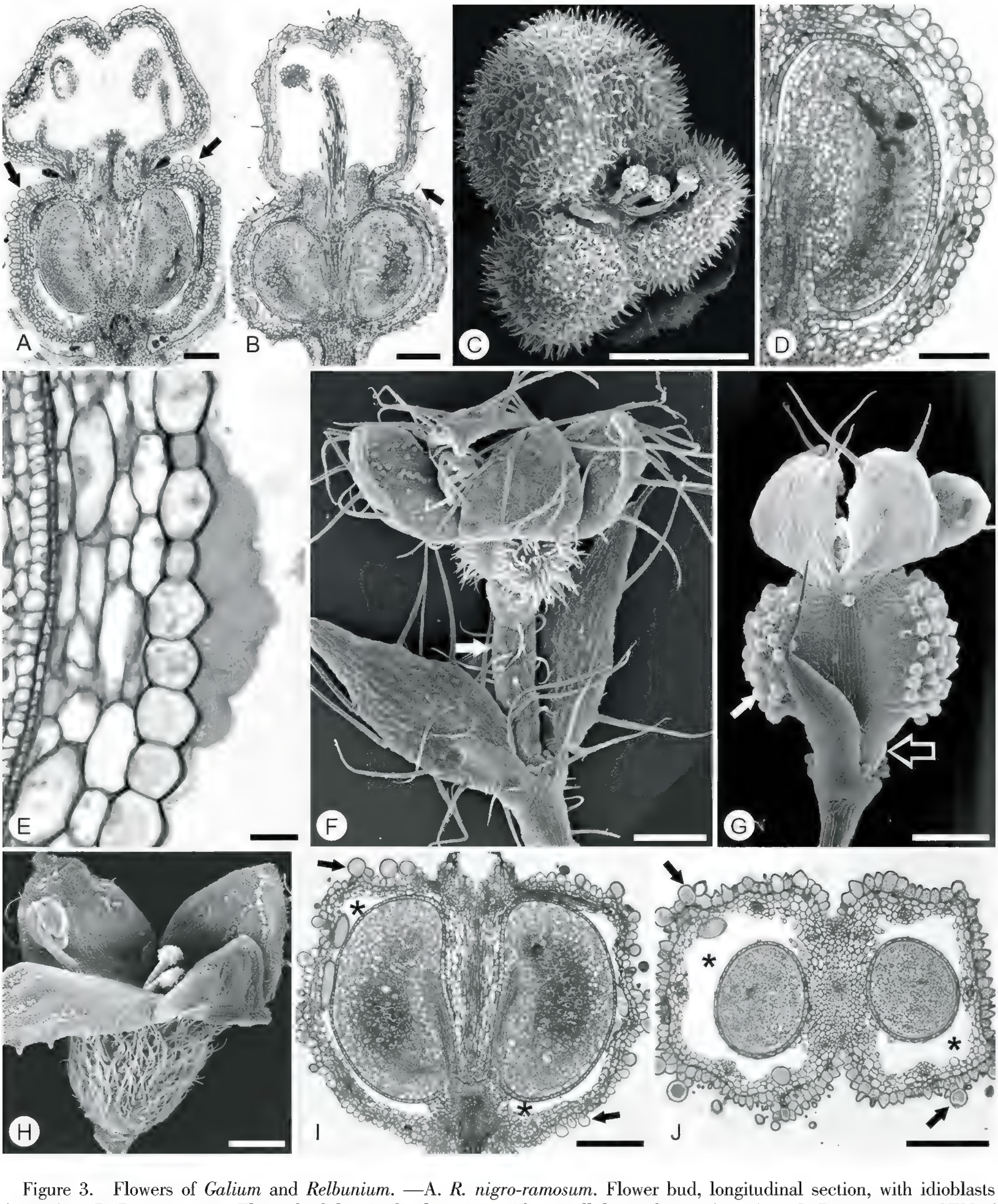

Figure 3. Flowers of *Galium* and *Relbunium*. —A. *R. nigro-ramosum*. Flower bud, longitudinal section, with idioblasts (arrows). —B. *R. ostenianum*. Flower bud, longitudinal section, with unicellular trichomes (arrow). —C. *R. ostenianum*. SEM of ovary after fertilization. —D. *R. humilioides*. Ovule, longitudinal section. —E. *R. hirtum*. Ovary wall with secretion accumulation (transverse section). —F. *R. humile*. SEM of flower with reduced pedicel (arrow). —G. *R. mazocarpum*. SEM of flower with reduced pedicel (black arrow) and idioblasts (white arrow). —H. *R. hypocarpium*. SEM of flower. —I. *G. uruguayense*. Ovary after fertilization, longitudinal section, with idioblasts (arrow) and pericarp lacunae (asterisks). —J. *R. megapotamicum*. Ovary, after fertilization, transverse section, with idioblasts (arrows) and pericarp lacunae (asterisks). Scale bars: D, E = 100 μm; J = 200 μm; A–C, F–I = 500 μm.

Periclinal divisions were observed in the carpel mesophyll of *Galium latoramosum*, in addition to the usual anticlinal divisions. Some cells on the external face of the epidermis divided in the periclinal plane, but did not constitute a bistratified epidermis. In both *Galium* and *Relbunium* species, the epidermis of the internal ovary face was invariably unistratified, having cells similar to those on the external epidermis, although smaller in size. This internal layer remained adjacent to the ovule. Before

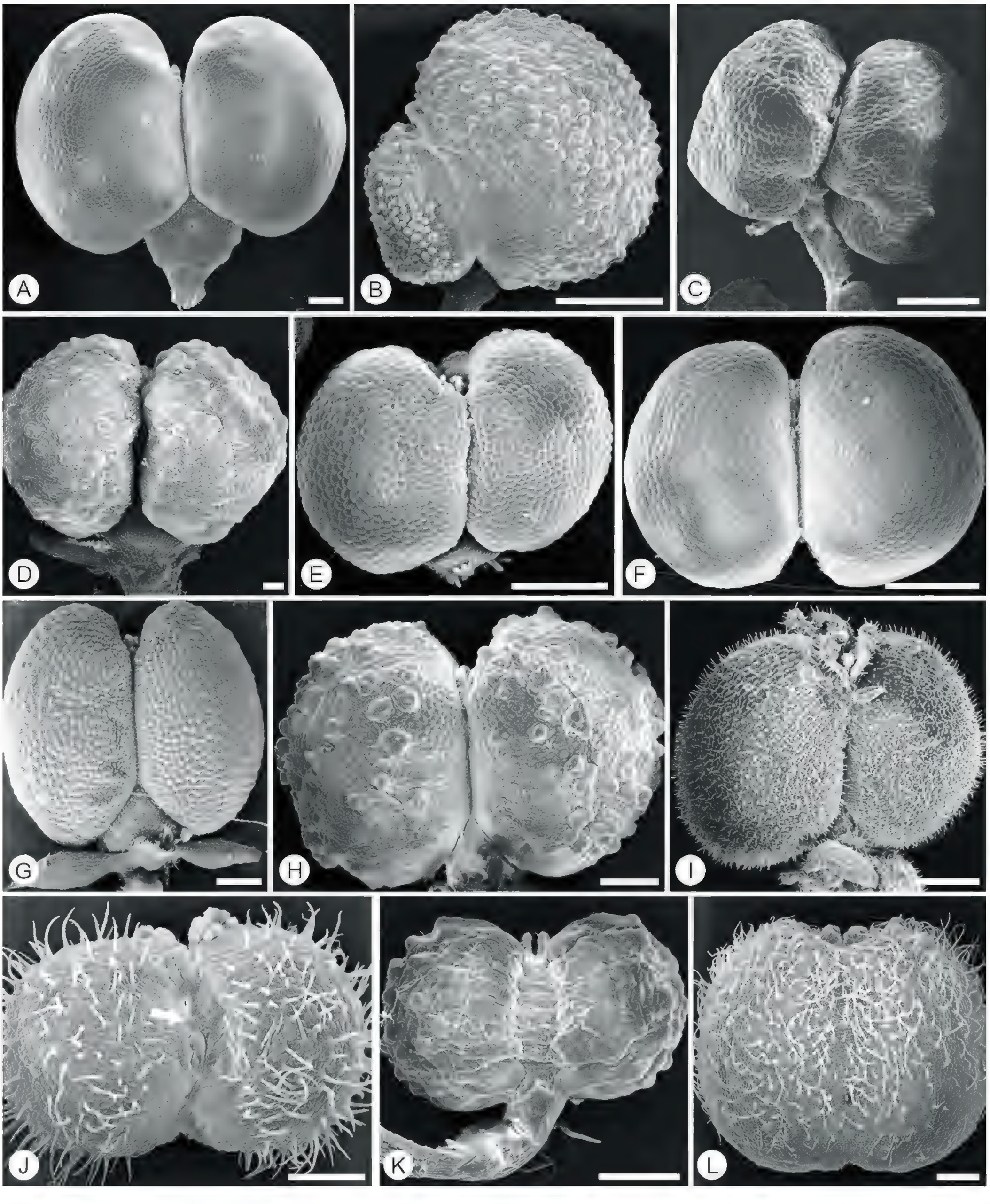

Figure 4. SEM fruits of *Galium* and *Relbunium*. —A. *R. valantioides*. —B. *G. uruguayense*. —C. *R. equisetoides*. —D. *R. nigro-ramosum*. —E. *R. humilioides*. —F. *R. hirtum*. —G. *R. longipedunculatum*. —H. *R. megapotamicum*. —I. *R. ostenianum*. —J. *R. humile*. Mericarp abscission region (arrows). —K. *R. mazocarpum*. —L. *R. hypocarpium*. Scale bars = 500 μm.

fertilization, large lacunae were formed by cellular lysis in the carpel mesophyll (Fig. 3I, J).

FRUITS

Fertilization may occur simultaneously in the two ovules or in only one; in both cases, fruits are formed, having either two (Fig. 4A) or only one mericarp (Fig. 4B), respectively. Two types of fruits were observed in *Relbunium*, schizocarps (Fig. 4A–K) and berries (Fig. 4L), with the latter only seen in *R. gracillimum* and *R. hypocarpium*. The early development of the two fruits was similar, differing relative to the pericarp succulence.

The tuberculate aspect of the fruit (Fig. 4B, D, H, K) in *Galium uruguayense* and three *Relbunium* species results from the presence of secretory idioblasts (Fig. 5A) covered by short striae of varying thicknesses (Fig. 5B). In *R. nigro-ramosum* and *R. megapotamicum*, the idioblasts are prominent in relation to the epidermis, and they are supported by two to three epidermal cells as well as mesocarp cells (Fig. 5C). The idioblasts occur isolated or in groups and range in size from five (*R. nigro-ramosum*, Fig. 4D) to 10 cells (*R. megapotamicum*, Fig. 4H). The cytoplasm of these cells appears very dense (Fig. 5A, C), indicating secretory activity. In *R. richardianum*, the cuticle becomes displaced by the accumulation of secretions between it and the external periclinal exocarp wall (Fig. 5G). Additional modifications of the other exocarp cells and cuticle were observed as the fruit continued to develop and the saliences of cuticle ridges and wrinkles (Fig. 5D) became distended and sparser (Fig. 5E). In *G. latoramosum*, the exocarp cells do not have ornamented cuticles (Fig. 5F).

In addition to idioblasts, unicellular trichomes were also observed on the exocarp of *Relbunium ostenianum* (Fig. 4I), *R. humile* (Fig. 4J), and *R. hypocarpium* (Fig. 4L). Other species, however, demonstrated fruits without idioblasts or trichomes, including *R. equisetoides* (Fig. 4C), *R. hirtum* (Fig. 4F), *R. humilioides* M. L. Porto & Ehrend. (Fig. 4E), *R. longipedunculatum* Mariath & Ehrend. (Fig. 4G), and *R. valantioides* (Cham. & Schltdl.) K. Schum. (Fig. 4A).

In early developmental stages, the mesocarp resembles the carpel mesophyll, except in *Galium latoramosum* and *Relbunium longipedunculatum*, which demonstrated an increase in cell layers, from five to eight, due to periclinal divisions (Fig. 5H). Until this stage is reached, the development of the two fruit types in *Relbunium* (schizocarps and berries) is similar. As seeds mature, however, structural differences can be observed in the pericarp, and these characteristics are therefore important in distinguishing among species of *Relbunium*.

In later developmental stages, the mesocarp of the schizocarpic fruit in *Relbunium* (Fig. 4A–K) reveals elongated cells with thin, and frequently obliterated, primary cell walls (Fig. 5K). Idioblasts with raphide crystals can be observed adjacent to the endocarp. In *R. equisetoides*, the mesocarp retains characteristics similar to the palisade parenchyma (Fig. 5J), as previously described for the ovary.

Similar to the exocarp, the endocarp cells slowly elongate during fruit maturation until the seed completes its development. The endocarp appeared greatly distended in *Galium uruguayense*, *Relbunium equisetoides*, *R. humilioides*, *R. valantioides*, *R. longipedunculatum*, and *R. megapotamicum*, although it remained intact and visible (Fig. 5I). Although the endocarp remained intact in *R. nigro-ramosum* and *R. ostenianum*, it was later almost imperceptible between the seed coat and the mesocarp (Fig. 5K). A discontinuity of the endocarp was observed in *G. latoramosum*, *R. richardianum*, *R. hirtum*, *R. humile*, and *R. mazocarpum*, in which the endocarp ruptured during fruit development and became obliterated and imperceptible (Fig. 5L).

During seed development, cellular digestion of the endosperm by the integument (Fig. 5M) and the endosperm by the embryo was observed, forming an endosperm digestion cavity (Fig. 5N). The integument was eventually almost entirely consumed, leaving only a single cell layer that formerly composed its external epidermis, or exotesta (Fig. 5I–K, O). The cytoplasm of the exotesta cells contained phenolic compounds in *Relbunium hirtum* (Fig. 5L), *R. longipedunculatum*, and *R. ostenianum*.

The endosperm appeared to be composed of homogeneous cells (Fig. 6A) with thickened cell walls composed principally of cellulose and pectins; significant quantities of lipids were observed in their cytoplasm. Additionally, a gradient of the cell wall thickness was observed in the endosperm, with the peripheral cells being much thicker than those closest to the embryo (Figs. 5L, 6B).

After embryo maturation, the schizocarpic fruit dehisces by the separation of the mericarps along an abscission line that divides them (Figs. 4J, 5N, 6A). This abscission region formed during the ovary development, with the contact between the two carpels giving rise to a zone of fragility. The cells in this region are parenchymatic, elongated, and have thin cell walls (Fig. 6C). Like schizocarpic fruits, berries also have distended exocarp and endocarp cells during development and maturation.

Idioblasts present on the external ovary epidermis (Fig. 2A) during the immature stages of the berry fruits of *Relbunium gracillimum* were not retained in the mature fruit (Fig. 6D), as fruit growth stretches the exocarp cells. However, trichomes present on the ovary and immature fruits of *R. hypocarpium* could still be observed on the mature fruits of this species (Fig. 4L).

The mesocarp appears succulent, having large, isodiametric parenchymatic cells with very thin cell walls and large vacuoles (Fig. 6E). Intercellular spaces were observed in *Relbunium hypocarpium*, but were absent in *R. gracillimum*. When the embryo reaches the torpedo stage, the mesocarp is composed

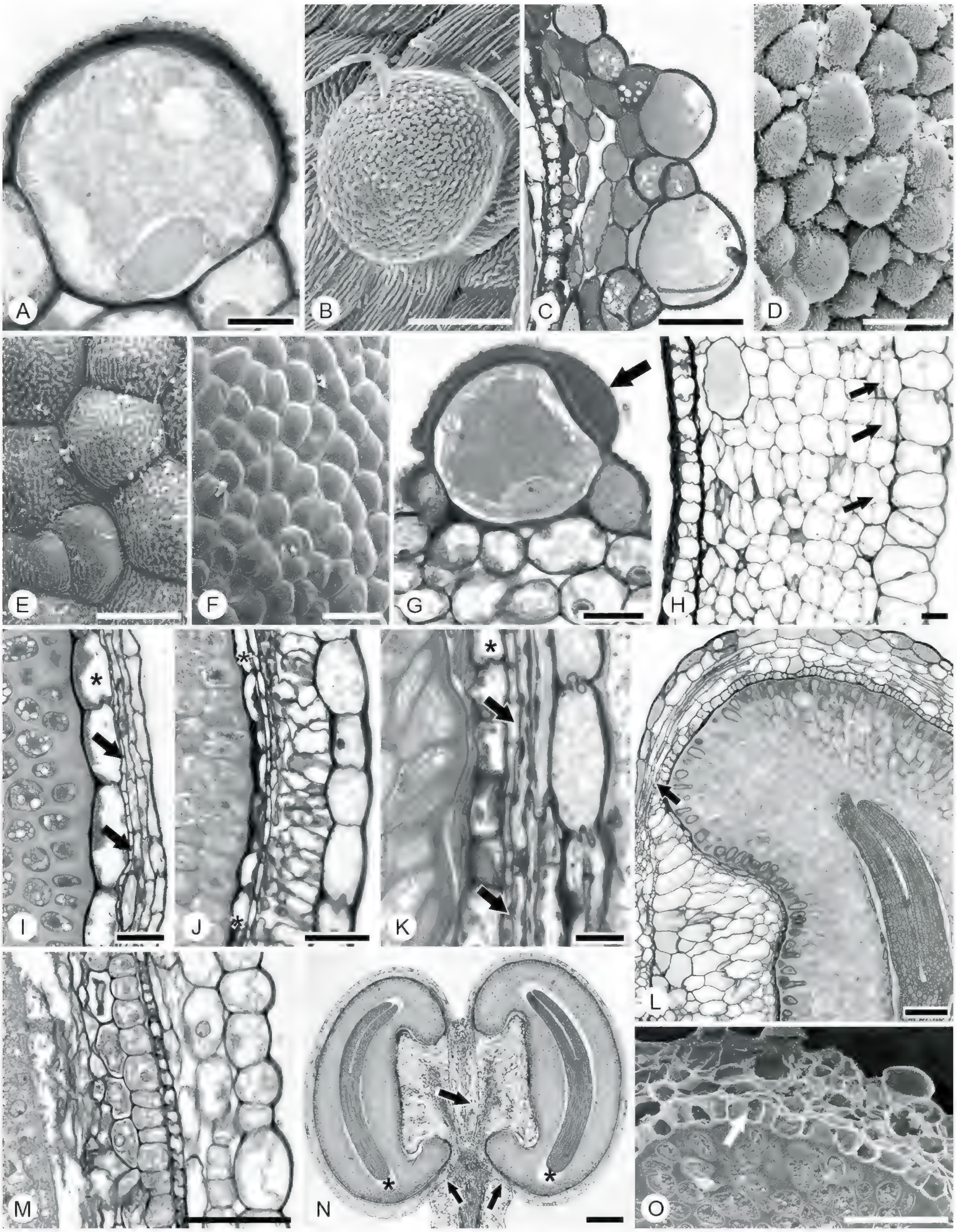

Figure 5. Fruits of *Galium* and *Relbunium*. —A. *G. uruguayense*. Idioblast detail, longitudinal section. —B. *G. uruguayense*. SEM of idioblast, frontal view. —C. *R. megapotamicum*. Pericarp with prominent idioblasts, longitudinal section. —D. *R. longipedunculatum*. SEM of epicuticular striae on exocarp, frontal view. —E. *R. longipedunculatum*. SEM of exocarp with epicuticular striae. —F. *G. latoramosum*. SEM of exocarp, frontal view. —G. *R. richardianum*. Secretion accumulation in idioblast (arrow), longitudinal section. —H. *G. latoramosum*. Pericarp with periclinal divisions (arrows), transverse section. —I. *G. uruguayense*. Pericarp evidencing endocarp (arrows) and seed coat (asterisk), transverse section. —J. *R. equisetoides*. General view of pericarp and seed coat (asterisks), transverse section. —K. *R. ostenianum*. Pericarp with endocarp (arrows) and seed coat (asterisk), transverse section. —L. *R. hirtum*. Mericarp section, with endocarp (arrows), longitudinal section. —M. *R. valantioides*. Early pericarp detail, transverse section, evidencing endosperm on integument cellular digestion. —N. *R. valantioides*. General fruit aspect, longitudinal section, with digestive cavity (asterisks) and abscission region (arrows). —O. *G. uruguayense*. Pericarp detail with seed coat (arrow). Scale bars: A, B, E, G = 50 μm; C, D, F, H–M, O = 100 μm; N = 500 μm.

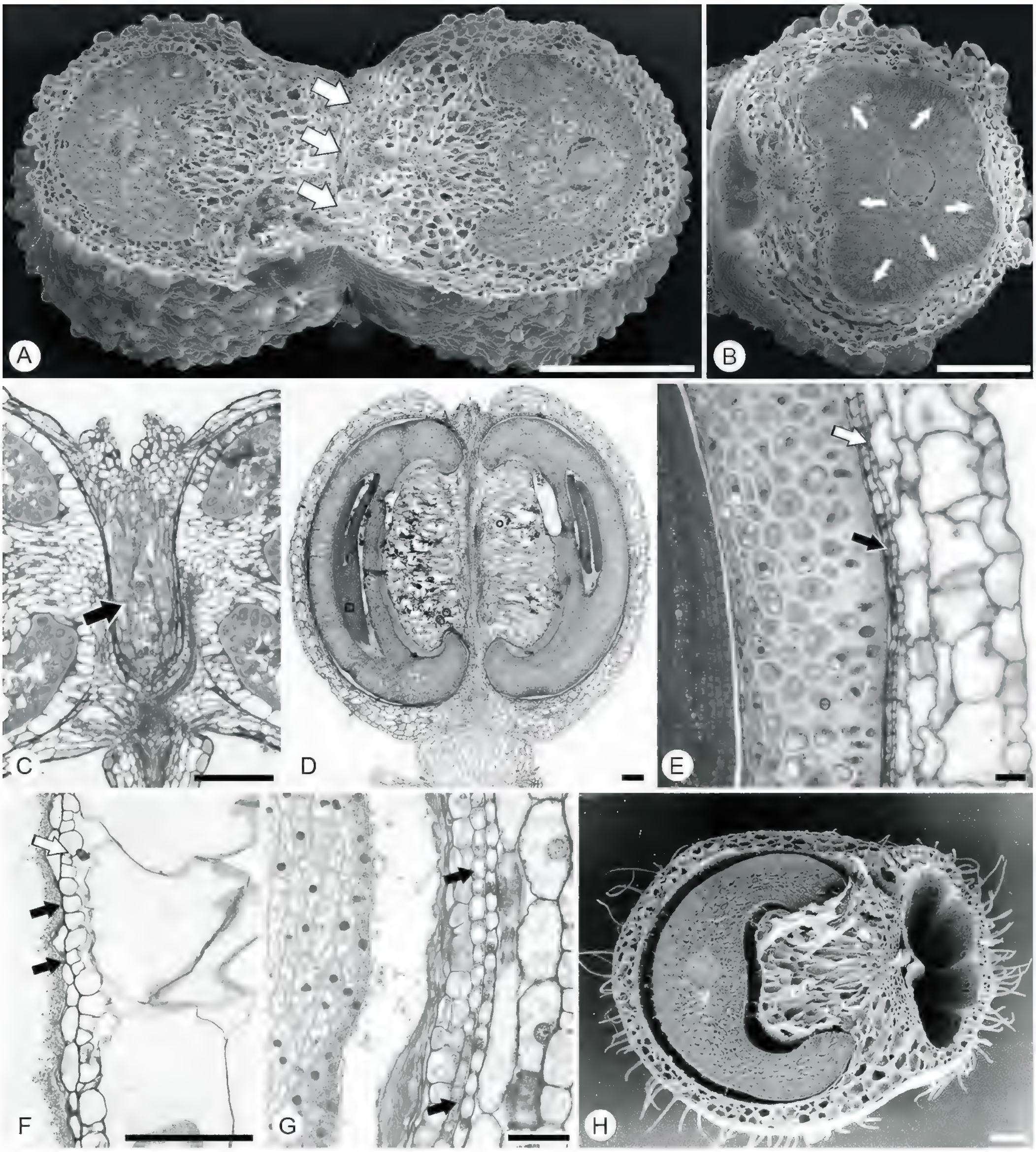

Figure 6. Fruits of *Galium* and *Relbunium*. —A. *G. uruguayense*. SEM of fruit, transverse section, with abscission region (arrows). —B. *R. megapotamicum*. SEM of mericarp, transverse section, endosperm cells with distinct wall thickness (arrows indicate edge of thicker cell walls). —C. *R. mazocarpum*. Fruit, longitudinal section, with mericarp abscission region detail (arrow). —D. *R. gracillimum*. Fruit, longitudinal section. —E. *R. gracillimum*. Pericarp, longitudinal section, with endocarp (white arrow) and seed coat (black arrow). —F. *R. hypocarpium*. Seed coat detail, transverse section, with fragmented portions (black arrows) and endocarp (white arrow). —G. *R. hypocarpium*. Pericarp detail, transverse section, with endosperm on integument cellular digestion. Cell layer that constitutes the exotesta (arrows). —H. *R. hypocarpium*. SEM of fruit, transverse section, with only one seed. Scale bars: F = 50 μm; C, E, G, H = 100 μm; A = 200 μm; B, D = 500 μm.

of three to five cell layers (Fig. 6D). Idioblasts with raphide crystals could be observed adjacent to the endocarp. The endocarp of the mature fruit remains intact, even after experiencing distension (Fig. 6E, F).

The exotesta was observed to form during endosperm digestion of the integument (Fig. 6G). During this phase, the ovule cell layers are digested, leaving only a single layer that covers the dorsal and ventral faces of the seed of *Relbunium gracillimum* (Fig. 6E). As in *R. gracillimum*, the exotesta of *R. hypocarpium* is composed of only a single cell layer, and it ruptures as the fruit grows, leaving fragments

attached to the endocarp (Fig. 6F). *Relbunium hypocarpium* is the only *Relbunium* species in which the seed is not uniformly enveloped by the exotesta.

The seeds of both schizocarp and berry fruits are elliptical to spherical, but schizocarp seeds have a slight sinuosity (Fig. 6B) not seen in berry seeds (Fig. 6H). A depression resulting from residual funicular tissue, which was not digested during endosperm formation, can be seen in the ventral region of the seeds (Fig. 6A, H). The torpedo phase embryo is curved and completely enveloped by the endosperm (Fig. 5N).

PHYLOGENETIC ANALYSES

Morphological data (Appendix 1) were used for parsimony analysis. The matrix comprised a total of 55 characters (Appendix 2). Of these 55 characters, six were considered variable, but without informative value for phylogenetic analysis, while 46 were considered parsimony informative. Parsimony analysis produced a phylogenetic tree 262 steps long, with a consistency index of 0.47 and a retention index of 0.51 (Fig. 7). This cladogram distinguished between the genera *Galium* and *Relbunium* based on the presence/absence of the fertile bracts, and the branch that included the two species of *Galium* was sister to all sampled *Relbunium*. Both clades share glandular trichomes on the adaxial corolla faces, schizocarpic fruits, and pericarp lacunae. The *Relbunium* clade is defined by the presence of a reduced pedicel and consists of two subclades (A and B), distinguished by having either four or two bracts, respectively.

Clade A in *Relbunium* is further partitioned into two species groupings—clade A1 and A2 (Fig. 7). The A1 species have imperceptibly reduced pedicels, while species of clade A2 have pedicels less than 0.7 mm long. *Relbunium equisetoides* lies basal in clade A1. This species differs from others in that the abaxial corolla face is glabrous and the fruit exocarp is ornamented with small saliences of cuticle ridges. The remaining species group of six shares an exocarp with a striate cuticle. Affined species consist of *R. richardianum*, *R. nigro-ramosum*, and *R. megapotamicum*. Two of these species (*R. nigro-ramosum* and *R. megapotamicum*) have fruits with parallel cuticular striae oriented toward the center of the epidermal cells forming a cuticular salience, as well as secretory idioblasts on the exocarp that are either isolated or united into clusters. *Relbunium richardianum* lies basal to these two species. *Relbunium nigro-ramosum* has bracts that are unequal in size, while the bracts of *R. megapotamicum* are uniform. A second affined group in clade A1 is united by the presence of tannin in the seed coat (*R. hirtum*, *R. ostenianum*, and *R. longipedunculatum*). The latter species differs in having pedunculate flowers with peduncles to 10–15 mm, and the fruit endocarp is continuous and remains intact during the entire phase of seed development. Sessile flowers and discontinuous endocarps distinguish both *R. hirtum* and *R. ostenianum*; however, they overtly differ in that *R. ostenianum* has two (or three) fertile bracts, while *R. hirtum* has four.

The four species that comprise clade A2 in *Relbunium* (Fig. 7) share an evident reduced pedicel and divide into two subgroups. The first consists of the species pair *R. gracillimum* and *R. hypocarpium*, with fleshy berries, while *R. humilioides* and *R. valantioides* have schizocarpic fruits. *Relbunium hypocarpium* differs from *R. gracillimum* in having unicellular trichomes on the external ovary face. *Relbunium humilioides* diverges from *R. valantioides* in having dispersed trichomes on the abaxial corolla face, ample intercellular spaces in the mesocarp, and an exocarp with short striae on the cuticle with no apparent orientation pattern. In contrast, in *R. valantioides*, the trichomes restrict to the margins of the abaxial corolla face, the intercellular spaces in the mesocarp are reduced and infrequent, and the exocarp cuticle is organized into long, parallel striae.

Clade B in *Relbunium* (Fig. 7) is composed of only two species, *R. humile* and *R. mazocarpum*. The pair lie sister to the other 11 exemplar species in *Relbunium* and basically differ by the presence of only two bracts and a prominent reduced pedicel. Of the pair, *R. mazocarpum* has fruits with secretory idioblasts on the exocarp, while in *R. humile* the exocarp is only pilose.

DISCUSSION

Despite studies focused on the genera *Galium* and *Relbunium*, their generic boundaries and respective species remain under discussion due to their significant morphological similarities. Additionally, many characteristics often used to distinguish the taxa of Rubiaceae are morphologically plastic and variable in response to their environments (Puff, 1975). Despite this, reproductive characteristics may remain consistently and systematically useful (Herr, 1984).

Galium has been distinguished by the following characteristics: a herbaceous and subshrubby habit; quadrangular stems; chartaceous to membranaceous leaves, with or without revolute margins (Dempster & Ehrendorfer, 1965); nodes with two opposite leaves, and two or more foliar stipules (Dempster, 1982); and

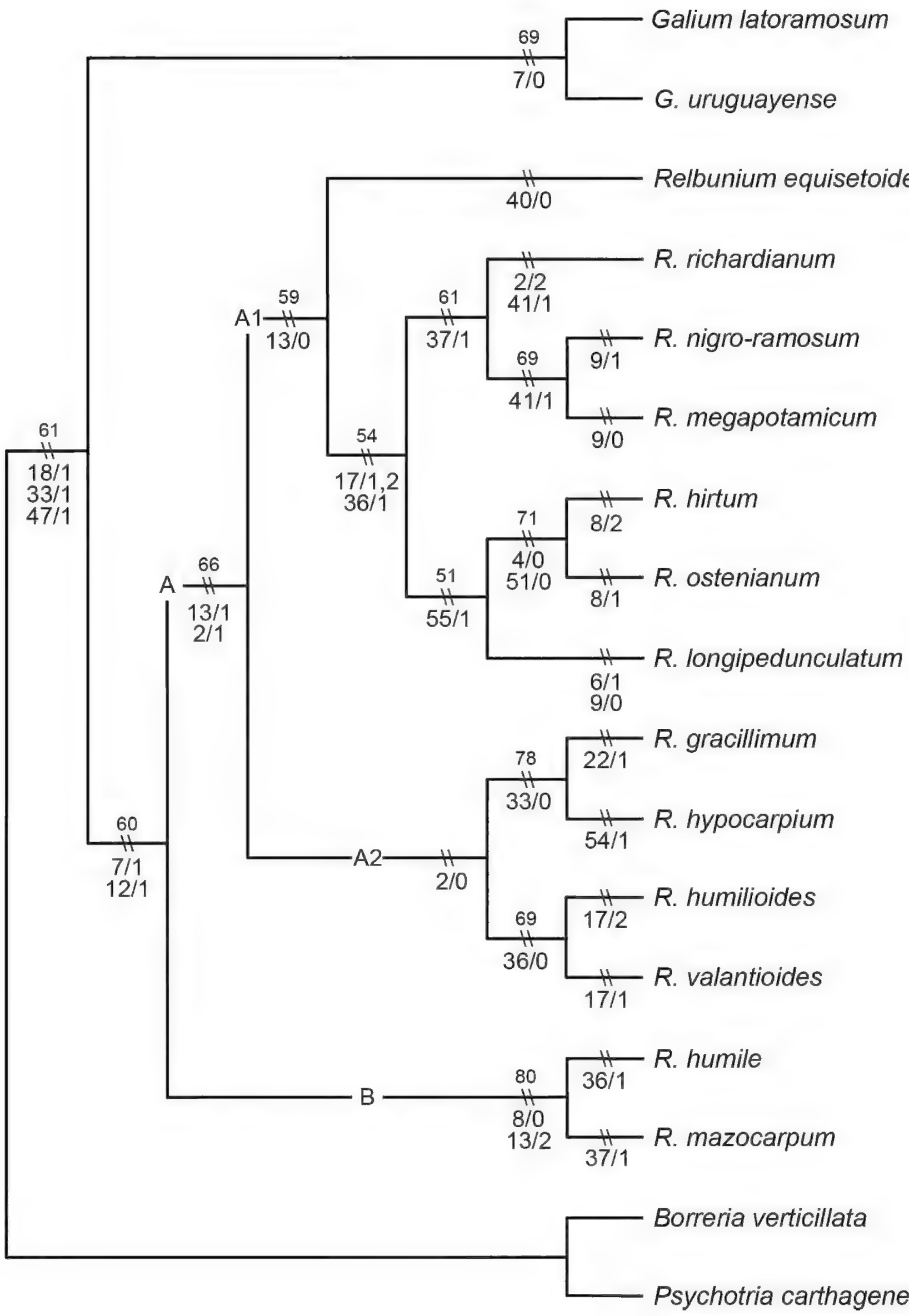

Figure 7. Parsimonious tree of *Galium* and *Relbunium* species derived from morphological data. Numbers above branches denote bootstrap percentages from 1000 replicates.

trichomes that are diminutive, retrorse, and more or less aculeate on the stems and leaves, but uncinate in the fruits (Dempster, 1981). The genus *Relbunium* is vegetatively similar to *Galium*. As such, reproductive morphologies can distinguish these two genera (Schumann, 1891; Ehrendorfer, 1955; Dempster, 1978).

In Rubiaceae, the basic inflorescence is the thyrse (Weberling, 1977), which is considered a plesiomorphic character within the family. Only the presence of solitary flowers, such as in *Relbunium*, might constitute a synapomorphy. However, in *Relbunium*, the appearance of inflorescences in two species may characterize a reversion, as observed in *R. equisetoides* and *R. richardianum*.

According to Robbrecht (1988), bracts are found in a majority of the inflorescences in Rubiaceae. Differing from many North American species, European species of *Galium* lack bracted inflorescences (Ehrendorfer, 1955). Species of *Galium* may sometimes have one or two bracts, such as *G. correllii* Dempster (Dempster, 1968), *G. wigginsii* Dempster

(Dempster, 1970), *G. ecuadoricum* Dempster, *G. ovalleanum* Phil., *G. trichocarpum* DC., *G. philippianum* Dempster (Dempster, 1980), *G. peruvianum* Dempster & Ehrend., *G. ferrugineum* K. Krause (Dempster, 1981), *G. araucanum* Phil., and *G. suffruticosum* Hook. & Arn. (Dempster, 1982). These species occur in North and Central America, with some to the western edge of the Andes Mountains to the south (Dempster, 1970, 1980, 1981, 1982).

This study documents the absence of bracts in *Galium latoramosum* and *G. uruguayense*. However, considering the presence of bracts in *Relbunium*, it should be noted that no variations of this characteristic were observed. Ehrendorfer (1955) and Detoni (1976) have suggested that the species of the genus *Relbunium* originated from New World species of *Galium*. Based on this hypothesis, we may infer that (1) the ancestors of *Relbunium* did not have bracts, and (2) because there is a north to south gradient in the number of bracts in the species of *Galium* through those American mountain ranges, the species that spread southward along the Andes gradually acquired them. Some of the species in northern California (U.S.A.) have one (or no) bracts (Dempster, 1968), while species from the southern region of this same state (Dempster, 1970, 1975) and in northern Mexico (Dempster, 1978) may have one to two bracts, and the number of bracts continues to increase along the Andes mountain chain, varying from two to four along its north to south distributional axis (Dempster, 1980, 1981, 1982).

As the presence of involucrate inflorescences is common in Rubiaceae (Robbrecht, 1988), it may be assumed that the absence of bracts in species of *Galium* represents a synapomorphy for that group, and consequently the presence of bracts in *Relbunium* represents a reversion with bracts separated from the flower by a reduced pedicel. These reduced pedicels were observed in the 13 species of *Relbunium* examined, although their lengths varied. From the cladogram (Fig. 7), it can be seen that the presence of a reduced pedicel is synapomorphic for the clade formed by *R. humile* and *R. mazocarpum*. Species with a prominent reduced pedicel were considered a basal group in *Relbunium*, indicating that the tendency toward elongating these structures is not a derived condition, but rather a plesiomorphic characteristic of the genus.

According to Ehrendorfer (1955), species of *Galium* do not have bracts, the flowers are overtly pedunculate, exceeding 15 mm, and the fruits have, in many cases, specialized trichomes. On the other hand, in *Relbunium*, the flowers have two to four bracts, are sessile or have short peduncles, and specialized trichomes are not observed on the fruits. Contrasted with observations of Ehrendorfer (1955), the present work noted the presence of long peduncles, at least 1.8 mm, on *Relbunium* flowers. However, *R. hirtum* and *R. ostenianum* demonstrated sessile flowers, thus confirming the importance of this characteristic to the phylogeny of the genus in the cladogram (Fig. 7).

Despite the fact that characters related to carpel development did not reveal differences between Rubiaceae taxa, fruit characteristics did indicate differences between the species of *Galium* and *Relbunium* analyzed. Different authors have described two types of pericarps: fleshy and dry. According to Eames and MacDaniels (1953), fruits with a fleshy pericarp are succulent and have parenchyma cells with thin walls that accumulate water in their vacuoles. Ergastic substances, such as starches, oils, and proteins, are frequently present, as well as calcium oxalate crystals and tannins (Roth, 1977). Based on these characteristics, among the species examined, only *G. latoramosum*, *R. gracillimum*, and *R. hypocarpium* have a fleshy pericarp. Fruits with a dry pericarp do not have a fleshy consistency (Font Quer, 1985), but do have sclerenchyma cells (Eames & MacDaniels, 1953) and dead cells when mature (Roth, 1977). However, the mesocarp of *G. uruguayense* and the *Relbunium* species cannot be considered dry according to this definition because they do not have cells with lignified cell walls and/or dead cells. These fruits have elongated cells with thin walls that remain alive and do not show secondary thickening, without, however, being succulent.

It is difficult to define the pericarps of the analyzed species as fleshy or dry, because they share characteristics with both and are considered intermediate. The mesocarp of *Pagameopsis* Steyerm. was considered to be more or less fleshy (Piesschaert et al., 2001). The pericarps of species of *Pentanisia* Harv. were described as rather succulent, although they have lignified portions (Puff & Robbrecht, 1989). In many Gardeniinae, the pericarp has been described as more or less dry (Robbrecht, 1988). According to Spjut (1994), the pericarp of fruits may sometimes be slightly fleshy or dry. Dempster (1990) indicated that the *Galium* fruits are relatively dry and that truly dry fruits are probably not found in this genus. Apparently, the fruits of *G. uruguayense* and the species of *Relbunium* are intermediate types with slightly dry pericarps (except for *G. latoramosum*, *R. gracillimum*, and *R. hypocarpium*, which have fleshy pericarps).

Rubiaceae demonstrate high morphological diversity in terms of its fruits, and phylogenetic studies have suggested that the ancestral fruit of the family was a many-seeded, dry capsule. It was then proposed by Bremer and Eriksson (1992) that fleshy fruits have arisen at least 12 times within the family, with four instances in Rubioideae and only one in Rubieae. Within this tribe, the tendency toward fleshiness is observed in *Didymaea* Hook. f., *Rubia*, and in some species of *Galium*. In *Galium*, and in related genera, fleshy fruits may have arisen from dry fruits after a reduction in seed number (Bremer & Eriksson, 1992). According to Bremer and Eriksson (1992), in *Relbunium gracillimum* and *R. hypocarpium* the fleshy fruits arose from dry fruits, being exclusive to and as a synapomorphy for the genus.

In comparing the pericarps of the *Relbunium* species analyzed here with those of *Rubia peregrina* L., *R. tinctorum* L., *Galium aparine* L., and *G. mollugo* L. described by Goursat and Guignard (1975), a transition from fleshy to dry pericarps can be inferred. *Rubia* is considered a sister group of the tribe (Manen et al., 1994), and the mesocarps of its species have many cell layers and a fleshy aspect, while in *Relbunium* there are fewer mesocarp layers and the fruits do not appear succulent. The number of mesocarp layers is even more reduced in *G. aparine* and *G. mollugo* (not more than three), and their fruits are schizocarps, although with a fleshy pericarp.

Fleshy and dry fruits, capsules, schizocarps, drupes, and berries are encountered within the Rubiaceae (Barroso et al., 1999). Roth (1977) classified the fruits of *Galium* as schizocarps, in accordance with Barroso et al. (1999), for the species of *Relbunium*. Schizocarpic fruits were first described by Schleiden (1837) for Apiaceae. Spjut (1994: 28–29) defined the fruits of *Galium* as an achenarium, a term that is synonymous with schizocarp, i.e., fruits that are derived from a schizocarp gynoecium, with indehiscent carpels that separate and represent distinct dispersal units (the mericarp). Many authors define schizocarp fruits as dehiscent, but this affirmation is conceptually equivocal. Because the pericarp does not rupture, with only a separation of the carpels being observed, they are, in fact, indehiscent (Spjut, 1994). Schizocarpic fruits in Rubiaceae are otherwise found in species of *Neopentanisia* Verdc. (Puff & Robbrecht, 1989) and in the genus *Scyphiphora* C. F. Gaertn. (Puff & Rohrhofer, 1993).

In addition to schizocarpic fruits, berries were observed in *Relbunium*, in *R. gracillimum* and *R. hypocarpium*. Berries, according to Barroso et al. (1999), are indehiscent fruits with fleshy and thin pericarps and undifferentiated endocarps. In the Rubiaceae, this type of fruit has been described for *Salzmannia* DC., *Coussarea* Aubl., *Faramea* Aubl., *Coccocypselum* P. Browne, *Schradera* Vahl, *Hippotis* Ruiz & Pav., *Hoffmannia* Sw., *Sabicea* Aubl., *Bertiera* Aubl., *Hamelia* Jacq., *Stachyarrhena* Hook. f., *Posoqueria* Aubl., *Gardenia* J. Ellis, *Randia* L., *Tocoyena* Aubl., *Genipa* L., *Amaioua* Aubl., *Melanopsidium* Colla, *Alibertia* A. Rich., *Borojoa* Cuatrec., *Kutchubaea* Fisch. ex DC., and *Duroia* L. f. (Barroso et al., 1999).

Variation was observed in both the seed morphology and the seed number per locule within Rubiaceae. The seed coat of Rubiaceae seeds is composed of an exotesta. This exotesta is composed of more than one cell layer in species of *Paragenipa* Baill. and *Didymosalpinx* Keay, although other genera have a reduced or absent exotesta (Robbrecht, 1988). When reduced, the exotesta appears as a membranaceous layer of cells with thin cell walls, located between the pericarp and the endosperm, as in *Callipeltis cucullaris* (L.) DC., *Sherardia arvensis* L. (Lloyd, 1902), *Oldenlandia alata* Roxb., *Dentella repens* (L.) J. R. Forst. & G. Forst. (Raghavan & Rangaswamy, 1941), *Borreria hispida* Spruce ex K. Schum. (Farooq, 1952), *O. corymbosa* L., *O. nudicaulis* Roth (Farooq, 1953), *Randia malabarica* Lam. (Periasamy, 1962), *Tarenna asiatica* Kuntze ex K. Schum. (Periasamy, 1964), *Anotis lancifolia* Hook. f. (Ahmad, 1978), *Dentella repens*, *D. serpyllifolia* Wall. ex Craib (Maheshwari & Raju, 1980), *Macrosphyra* Hook. f., *Argocoffeopsis* Lebrun, *Calycosiphonia* Robbr., *Craterispermum* Benth., and the Aulacocalyceae tribe (Robbrecht, 1986). Mariath (1990) described the seeds of *Relbunium hypocarpium* as lacking a seed coat, although De Toni and Mariath (1999) described a thin and sometimes discontinuous layer of cells corresponding to the exotesta for the same taxa. In analyzing the species of *Galium* and *Relbunium* in this paper, the presence of at least one cell layer covering the endosperm was confirmed, thus characterizing an exotesta, in agreement with De Toni and Mariath (1999).

Manen et al. (1994) characterized the tribe Rubieae as monophyletic and recognized the formation of five clades, including *Rubia*, *Sherardia* L., *Asperula* L. sect. *Glabella* clade, *Cruciata* Mill., and *Galium* L. sect. *Galium*. This analysis placed species of *Galium* in three of the five clades established. Manen et al. (1994) and Bremer and Manen (2000) viewed the genus as of probable paraphyletic origin, while Manen and Natali (1995) considered *Galium* polyphyletic. These differences of opinion with

relation to the origin of these taxa are to be expected, as the genus comprises more than 400 species. Bremer and Manen (2000) defined *Relbunium* as a monophyletic group among the Rubieae, which agrees with the morphological data presented here.

Dempster prepared an ample revision of *Galium* species from North, South, and Central America (Dempster & Ehrendorfer, 1965; Dempster, 1968, 1970, 1975, 1978, 1980, 1981, 1982, 1990). For the South American taxa, Dempster (1982, 1990) discussed the validity of *Relbunium* as a genus and considered it to be a section of the genus *Galium*. Endlicher (1839: 523) proposed the name *Relbunium* as a section of *Galium*, based on de Candolle (1839) for *Rubia* sect. *Involucratae*, and described it as: "...Pedunculi axillares apice gerentes bracteas quatuor verticillatas, involucrum constituentes, flores intra involucrum solitarii v. terni, sessiles v. pedicellati." Dempster (1982) observed that this definition allowed the generic inclusion of not only sessile involucrate flowers, but also involucrate inflorescences. This author affirmed that Endlicher's reference to pedicellate flowers actually referred to branchlets instead of true pedicels. It is worth noting that Dempster did not refer to the pedicels of the flowers of *Relbunium* as true pedicels, since the presence of bracts obliged this author to define them as false pedicels. It may be inferred that Dempster assumed Endlicher permitted the inclusion of flowers with true pedicels (those without bracts) in *Relbunium*. Therefore, it is easy to understand why Dempster mentioned that Endlicher did not refer to the pedicels with bracts as being true pedicels. However, in the description presented by Endlicher (1839), one cannot perceive any mention of pedicellate flowers without bracts, a condition defined by Dempster as being critical in the decision to validate *Relbunium*.

When later elevating *Relbunium* to a genus, Bentham and Hooker (1873: 149) described it as: "...Herbae habitu follis floribusque Galli, flores bracteis 4 involucrati, sed inflorescentia involucrata, fructuque saepissime carnoso, pedicello cum calyce articulato..." In agreement with Dempster (1982), these authors continued to accept the permissive definition of Endlicher and to include flowers without bracts into *Relbunium*. Ehrendorfer (1955: 518) provided a more detailed description without altering the significance of the previous proposals: "...Flores sessiles vel rarius brevissime pedicellati, bracteis quaternis vel binis involucrati; bracteae involucrales nonnunquam ipsae pedunculos gerentes." Dempster (1982: 212–213) affirmed that, in using the word "peduncles" in this description, Ehrendorfer was emphasizing that these species had branchlets with true pedicels. However, the presence of bracts is sufficient evidence to maintain *Relbunium* as genus in this paper, given the relevance of this character in defining the group.

In contrast, Dempster (1982) determined that the flowers in *Relbunium* are individually involucrate and/or sessile. As such, this author transferred the species of *Relbunium* that did not have involucrate inflorescences (*R. richardianum*, *R. equisetoides*, and *R. diphyllum* K. Schum.) to *Galium*, affirming these species as similar to *G. suffruticosum*, *G. araucanum* (Dempster, 1982), *G. microphyllum* A. Gray, and *G. corymbosum* Ruiz & Pav. (Dempster, 1990). Dempster (1982) observed such variation among these species of *Galium*, such as occasional bracts at the base of the inflorescences, thus giving rise to the *G. richardianum* (Gillies ex Hook. & Arn.) Endl. complex (Dempster, 1982). This *G. richardianum* complex fills a gap that exists between the genera *Relbunium* and *Galium*, as all of the individuals of *G. suffruticosum* have flowers with pedicels, while the otherwise similar species *G. araucanum* has sessile flowers, as seen in some *Relbunium* species. However, *G. araucanum* (like *G. richardianum*) has few flowers with bracts. There are many similarities between *G. araucanum* and *G. richardianum*, and these two species differ principally in terms of the surfaces of their fruits, which are tuberculate in *G. richardianum* and smooth in *G. araucanum*. Thus, involucrate, sessile, and solitary flowers probably originated from the primitive pedicellate and cymose condition in *Galium* (Dempster, 1982). In 1990, Dempster transferred ca. 12 species of *Relbunium*, including them in *Galium*.

The generic segregation of *Relbunium* from *Galium* has been confirmed by the work of Detoni (1976) and Cavalli (1976), who used analyses of flavonoids and isozymes and indicated that *R. hypocarpium* was the most basal species of its genus at that time. The current morphological evidence confirms the segregation of *Relbunium* from *Galium* and maintains *Relbunium* as an autonomous genus. However, the basal position of *R. hypocarpium* within the genus could not be confirmed by the morphological characteristics of the reproductive organs, because that position is occupied by *R. humile* and *R. mazocarpum*.

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APPENDIX 1. Morphological characters and character states in *Galium* and *Relbunium*. Compare Appendix 2 and Table 1 for species exemplars.

1. Flower: (0) bisporic, (1) monosporic.
2. Inflorescences: (0) absent, (1) present, (2) both inflorescences and solitary flowers present.
3. Inflorescence morphology: (0) monochasium, (1) dichasium, (2) panicle, (3) pseudanthia.
4. Peduncle: (0) absent, (1) present.
5. Peduncle: (0) to 5 mm (short), (1) 5–10 mm (medium), (2) 10–15 mm (long), (3) to 20 mm (longer).
6. Floral peduncle: (0) erect, (1) curved.
7. Floral bracts: (0) absent, (1) present.
8. Bract number: (0) 2, (1) 2 or 3, (2) 4.
9. Bract presentation: (0) equal, (1) unequal.
10. Bract shape: (0) wider than long, (1) longer than wide.
11. Bract position: (0) not enveloping flowers and fruits, (1) enveloping flowers and fruits.
12. Reduced pedicel: (0) absent, (1) present.
13. Reduced pedicel: (0) imperceptible, (1) less than 0.7 mm, (2) 0.7–1.1 mm.
14. Calyx: (0) evident, (1) reduced, (2) absent.
15. Corolla shape: (0) campanulate, (1) infundibular, (2) rotate.
16. Corolla epidermal cuticle surface: (0) wrinkled, (1) striate.
17. Corolla abaxial epidermis, unicellular trichomes: (0) absent, (1) marginal, (2) dispersed.
18. Corolla adaxial epidermis, trichomes: (0) unicellular, (1) glandular.
19. Corolla, glandular trichomes: (0) dispersed, (1) marginal and along central vein.
20. Corolla, marginal glandular trichomes in: (0) 1 row, (1) 2 or 3 rows, (2) 3 to 5 rows.
21. Corolla, glandular trichomes along the central vein in: (0) 1 row, (1) 2 or 3 rows.
22. Corolla abaxial epidermis, idioblasts: (0) absent, (1) present.
23. Corolla mesophyll: (0) 2 to 4 layers, (1) 4 to 6 layers, (2) more than 6 layers.
24. Corolla mesophyll, intercellular spaces: (0) reduced, (1) abundant.
25. Corolla mesophyll, crystalliferous idioblasts: (0) next to adaxial epidermis, (1) in the mesophyll.
26. Ovary, periclinal external wall of epidermal cells: (0) plain, (1) rounded.
27. Ovary, cuticle of the epidermal cells: (0) wrinkles, (1) striae.
28. Ovary, striae orientation: (0) random, (1) parallel, (2) into the cell center.
29. Ovary: (0) glabrous, (1) pubescent.
30. Ovary, with idioblasts: (0) absent, (1) present.
31. Ovary, rounded appearance to epidermal cells: (0) absent, (1) present.
32. Fruits with the reduced pedicel: (0) not elongating, as in the flowers, (1) elongating in fruit, longer than in flowers.
33. Fruits: (0) fleshy, (1) dry.
34. Fruits fleshy and as: (0) berry, (1) drupe.
35. Fruits dry and as: (0) septicidal capsules, (1) schizocarp.
36. Exocarp: (0) glabrous, (1) pubescent.
37. Fruits with the idioblasts: (0) absent, (1) present.
38. Exocarp cells with periclinal divisions: (0) absent, (1) present.

39. Exocarp with papillae: (0) absent, (1) present.
40. Exocarp idioblasts with: (0) striae short cuticle, (1) striae long cuticle.
41. Exocarp idioblasts: (0) isolated, (1) isolated and in groups.
42. Mesocarp cells: (0) isodiametric, (1) elongated.
43. Mesocarp, cellular layers in early fruits: (0) 3 to 5, (1) 4 to 7, (2) more than 7.
44. Mesocarp, cellular layers in mature fruits: (0) 2 to 3, (1) 4 to 6, (2) 7 to 10, (3) more than 10.
45. Mesocarp, periclinal divisions: (0) absent, (1) present.
46. Mesocarp, cells: (0) isodiametrics, (1) as palisade tissue.
47. Mesocarp, lacunae: (0) absent, (1) present.
48. Mesocarp, intercellular spaces: (0) not frequently, (1) very frequently.
49. Mesocarp, succulent: (0) absent, (1) present.
50. Endocarp, single layer: (0) absent, (1) present.
51. Endocarp: (0) discontinuous, (1) continuous.
52. Endocarp entire: (0) visible, (1) invisible.
53. Seed coat: (0) single layer of cells, (1) more than one layer.
54. Seed coat, cellular layer: (0) entire, (1) fragmented.
55. Seed coat, cells: (0) without tannin drops, (1) with tannin drops.

APPENDIX 2. Morphological matrix. In addition to numerical character states, polymorphic characters are represented as ? = unknown state, – = inapplicable.

Species	Characters
	1 10 20 30 40 50 55
Galium latoramosum	1 2 1 1 0 0 0 – – – – 0 – 2 2 0 0 1 1 2 1 0 0 0 0 0 1 1 0 0 0 – 1 – 1 0 0 1 0 – – 0 1 2 1 0 1 0 1 1 0 – 0 0 0
G. uruguayense	0 0 – 1 0 0 0 – – – – 0 – 2 2 0 2 1 0 – – 0 0 0 0 0 1 1 0 1 0 – 1 – 1 0 1 0 0 0 0 1 1 0 0 0 1 1 0 1 1 0 0 0
Relbunium equisetoides	0 1 1 1 0 0 1 2 1 1 0 1 0 2 2 0 0 1 1 1 0 0 0 1 0 0 0 – 0 0 0 0 1 – 1 0 0 0 0 – – 1 0 0 0 1 1 1 0 1 1 1 0 0 0
R. gracillimum	0 0 – 1 2 0 1 2 0 1 0 1 1 2 2 ? 0 1 1 ? ? 1 0 0 0 1 0 – 0 1 1 0 0 0 – 0 0 0 0 – – 0 0 0 0 0 1 0 1 1 1 0 0 0 0
R. hirtum	0 0 – 0 – – 1 2 0 1 0 1 0 2 2 1 2 1 1 0 0 0 1 0 0 1 0 – 0 0 1 0 1 – 1 0 0 0 1 – – 1 0 0 0 0 1 0 0 1 0 – 0 0 1
R. humile	0 0 – 1 0 0 1 0 0 1 0 1 2 2 2 0 1 1 1 1 0 0 0 1 0 0 1 1 1 0 0 1 1 – 1 1 0 0 0 – – 1 0 0 0 0 1 0 0 1 0 – 0 0 0
R. humilioides	0 0 – 1 1 0 1 2 0 0 1 1 1 2 2 0 2 1 1 1 0 0 1 1 1 1 1 0 0 0 1 0 1 – 1 0 0 0 0 – – 1 0 0 0 0 1 1 0 1 1 0 0 0 0
R. hypocarpium	0 0 – 1 2 0 1 2 0 0 0 1 0 2 2 0 1 1 1 1 1 0 0 1 0 0 0 – 1 0 0 0 0 0 – 1 0 0 0 – – 0 0 0 0 0 1 0 1 1 1 0 0 1 0
R. longipedunculatum	0 0 – 1 2 1 1 2 1 1 0 1 1 2 2 0 0 1 1 2 1 0 1 0 0 1 1 1 0 0 1 0 1 – 1 0 0 0 1 – – 1 0 2 0 0 1 0 0 1 1 0 0 0 1
R. mazocarpum	0 0 – 1 0 1 1 0 0 1 0 1 2 2 2 0 1 1 1 1 0 0 0 1 0 0 1 1 0 1 0 1 1 – 1 0 1 0 0 1 0 1 0 0 0 0 1 0 0 1 0 – 0 0 0
R. megapotamicum	0 0 – 1 0 0 1 2 0 1 0 1 0 2 2 0 0 1 1 1 0 0 1 0 0 0 1 2 0 1 1 0 1 – 1 0 1 0 1 1 1 1 0 0 0 0 1 1 0 1 1 0 0 0 0
R. nigro-ramosum	0 0 – 1 0 0 1 2 1 1 0 1 0 2 2 1 0 1 1 1 0 0 1 0 0 1 1 2 0 1 1 0 1 – 1 0 1 0 0 1 1 1 1 1 0 0 1 1 0 1 1 0 0 0
R. ostenianum	0 0 – 0 – – 1 1 0 1 0 1 0 2 2 0 2 1 1 1 1 0 1 0 1 0 1 2 1 0 1 0 1 – 1 1 0 0 1 – – 1 1 1 0 0 1 0 0 1 1 1 0 0 1
R. richardianum	0 2 0 1 0 0 1 2 0 1 0 1 0 2 2 0 0 1 1 1 0 0 1 0 0 0 1 0 0 1 1 0 1 – 1 0 1 0 1 0 0 1 1 0 0 0 1 0 0 1 0 – 0 0 0
R. valantioides	0 0 – 1 1 0 1 2 0 0 1 1 1 2 2 0 1 1 1 1 0 0 1 0 0 0 1 1 0 0 0 0 1 – 1 0 0 0 0 – – 1 0 0 0 0 1 0 0 1 1 0 0 0 0
Borreria verticillata	0 1 3 0 – – 1 2 0 1 0 0 – 0 1 ? 2 ? ? ? ? ? 0 2 1 0 0 ? ? 1 0 0 – 1 – 0 1 0 0 0 – – 1 2 1 0 0 0 0 0 0 1 0 0 0 1
Psychotria carthagenensis	0 1 2 1 3 0 1 0 0 1 0 0 – 1 0 ? 2 ? ? ? ? ? 0 2 1 0 0 ? ? 0 0 0 – 0 1 – 0 0 0 0 – – 0 2 3 1 0 0 0 1 0 1 0 1 0 0

THE *INDEX TO PLANT CHROMOSOME NUMBERS* (IPCN): THREE DECADES OF PUBLICATION BY THE MISSOURI BOTANICAL GARDEN COME TO AN END

Peter Goldblatt[1] *and Porter P. Lowry II*[1,2]

The *Index to Plant Chromosome Numbers* (IPCN) was conceived in the 1950s by botanists at the University of California, Berkeley, as an index to all original plant chromosome counts published in the world's literature. At the time, the value of chromosome information was increasing for the insights that cytology provided about relationships and evolutionary pathways, and new counts were accumulating rapidly. The *Index* was seen as a complement to the earlier *Chromosome Atlas of Flowering Plants* by Darlington and Wylie (1955) and the equally valued *Chromosome Atlas of Cultivated Plants* by Darlington and Janaki Amal (1945).

Preparation of annual indexes, supported initially by a grant from the National Science Foundation (NSF), was coordinated by Marion S. Cave (UC, Berkeley), who served as editor from 1956 through 1964 (Cave, 1958–1959, 1961–1965). The project depended largely on a team of voluntary reviewers, each assigned a set of journals to review for chromosome counts. The IPCN project moved to the Biosystematics Research Institute, Canada Department of Agriculture, in about 1966, where under R. J. Moore's editorship, indexes were published covering 1967 to 1974 (Moore, 1970, 1971, 1972, 1973, 1974, 1977). Moore's last contribution was a combined 1973–1974 index (Moore, 1977), after which ill health forced him to relinquish editorship and IPCN actually ceased to function for some years.

In 1978, the IPCN project formally moved to the Missouri Botanical Garden, under the editorship of Peter Goldblatt, who had offered to take on the project, and who secured a series of grants from the NSF beginning in 1978 to finance the preparation and publication of chromosome indexes. In 1987, Dale E. Johnson, a long-time reviewer for the project, joined as co-editor. Data entry via TROPICOS with software developed by Bob Magill began with the 1982 index, and all counts published thereafter are databased and available online.

After 2005, proposals to the NSF for continued support of the project were declined and it became clear that the NSF would no longer fund such endeavors. Preparation of the most recently published index (2004–2006) (Goldblatt & Johnson, 2010) was funded entirely by the Missouri Botanical Garden (salary for data entry personnel, Goldblatt's time coordinating IPCN, Magill's time for software development). From the outset, publication costs were always funded by the Garden, with some or all of the costs being recovered through sales.

Financial constraints in 2009 and 2010 resulted in plans to release the 2004–2006 *Index*, then in proof stage, electronically rather than as a print publication. In response to this plan, Tod Stuessy (International Association for Plant Taxonomy [IAPT] Secretary and Professor of Botany at University of Vienna) indicated that he considered the IPCN to be an invaluable service to the botanical community (see also Fay, 2011) and that he regarded print publication of indexes as essential. He thus offered to assume responsibility for publication of IPCN in the IAPT serial *Regnum Vegetabile*, starting with the 2004–2006 *Index* (the latest IPCN volume, published in December 2010).

Professor Stuessy has undertaken to find a new home for IPCN, although to date no one has indicated a willingness to assume editorship of the project. At his bidding, in August 2010 Goldblatt forwarded all reviewing information to Karol Marhold at IAPT, who is assuming the editorship on an interim basis, and he informed all IPCN reviewers about the planned new editorship.

In an effort to maintain smooth production of IPCN, Professor Stuessy offered a modest annual

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subsidy to the Missouri Botanical Garden to cover the cost of further data entry, with the understanding that downloads would be sent to IAPT for publication of future indexes. Professor Stuessy understands the importance of continuing to build the IPCN database and of maintaining its integration within TROPICOS, and he supports the Garden's willingness to do so.

Over a span of more than three decades, the Missouri Botanical Garden regularly published the *Index to Plant Chromosome Numbers*, beginning with the index for 1975–1978 and ending with the index for the years 2004–2006 (Goldblatt, 1981, 1984, 1985, 1987; Goldblatt & Johnson, 1990, 1991, 1994, 1996, 1998, 2000, 2003, 2006, 2010). Responsibility for the project has now been successfully transferred to IAPT, closing an important chapter in the history of the Missouri Botanical Garden's contribution to botanical knowledge and service to the research community.

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CONTRIBUCIÓN AL CONOCIMIENTO DE LAS ESPECIES DEL GÉNERO *AXONOPUS* (POACEAE, PANICOIDEAE, PANICEAE) PARA SUDAMÉRICA AUSTRAL[1]

Diego L. Salariato,[2] *Fernando O. Zuloaga*[2] y *Osvaldo Morrone*[2]

Resumen

En la presente contribución se revisan por primera vez 31 especies de *Axonopus* P. Beauv. (Poaceae) para Argentina, el sur de Brasil, Bolivia, Chile continental, Paraguay y Uruguay. Se proveen de descripciones detalladas, una clave para la identificación de los taxones, ilustraciones, distribuciones y afinidades morfológicas de las especies. Se cita por primera vez *A. caulescens* (Mez) Henrard para Bolivia, y se incluyen los nombres *A. eminens* (Nees) G. A. Black y *A. kleinii* L. B. Sm. & Wassh. en la sinonimia de *A. siccus* (Nees) Kuhlm. y *A. uninodis* (Hack.) G. A. Black, respectivamente. Se lectotipifican a *Panicum hagenbeckianum* Kuntze y a *Paspalum ulei* Hack.

Abstract

The present treatment includes the first revision of 31 species of *Axonopus* P. Beauv. (Poaceae) in Argentina, southern Brazil, Bolivia, continental Chile, Paraguay, and Uruguay. A key to the species is provided, together with detailed descriptions, illustrations, distribution ranges, and a discussion of the morphological relationships of the species. *Axonopus caulescens* (Mez) Henrard is first reported for Bolivia, and the names *A. eminens* (Nees) G. A. Black and *A. kleinii* L. B. Sm. & Wassh. are synonymized with *A. siccus* (Nees) Kuhlm. and *A. uninodis* (Hack.) G. A. Black, respectively. The names *Panicum hagenbeckianum* Kuntze and *Paspalum ulei* Hack. are lectotypified.

Key words: *Axonopus*, Paniceae, Poaceae, South America.

El género *Axonopus* P. Beauv. se reconoce principalmente por sus espiguillas agrupadas unilateralmente en inflorescencias racemosas, solitarias y adaxiales (con la lema superior opuesta al eje del raquis) y por la ausencia de la gluma inferior. *Axonopus* pertenece a la tribu Paniceae, de la subfamilia Panicoideae, y es uno de los géneros más numerosos de la tribu junto con *Panicum* L., *Paspalum* L. y *Setaria* P. Beauv. Dentro de la tribu Paniceae, *Axonopus* presenta afinidades morfológicas con *Paspalum*, distinguiéndose ambos géneros por la orientación de la espiguilla en relación al raquis (abaxial en *Paspalum*). *Axonopus* también es superficialmente similar a *Digitaria* Haller, pero este último taxón se aparta por tener espiguillas agrupadas en pares y con orientación abaxial.

Si bien *Axonopus* se distingue claramente a nivel genérico, la delimitación de sus especies y los grupos infragenéricos es más dificultosa. El género ha sido subdividido, sobre la base de los caracteres exomorfológicos, en secciones y/o series y subseries por diferentes autores (Chase, 1911; Pilger, 1940; Black, 1963; Clayton & Renvoize, 1986; Giraldo-Cañas, 2000, 2001, 2007). Desde el punto de vista citológico, *Axonopus* se caracteriza por tener un número básico de cromosomas $x = 10$ y diferentes niveles de ploidía, con aproximadamente un 80% de especies poliploides (Giraldo-Cañas, 2008a) y números cromosómicos que varían desde $2n = 2x = 20$ a $2n = 10x = 100$.

Hasta el presente, los estudios filogenéticos en el género, sobre la base de datos morfológicos, han resultado poco informativos en relación a las relaciones supra- e infragenéricas. Por ello, las

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relaciones de *Axonopus*, dentro de la tribu Paniceae, no están aún resueltas (Zuloaga et al., 2000). Aliscioni (2002), en un análisis filogenético del género *Paspalum* basado también en caracteres morfológicos, postula que *Axonopus* podría ser incluido en *Paspalum*. Giraldo-Cañas (2007) señala, en un estudio filogenético de *Axonopus*, que la serie *Barbigeri* G. A. Black es monofilética.

Los análisis moleculares llevados a cabo en la tribu Paniceae, y que han incluido una escasa representación de especies de *Axonopus*, muestran al género como monofilético (Gómez-Martínez & Culham, 2000; Giussani et al., 2001). En estas contribuciones, *Axonopus* aparece relacionado (Gómez Martínez & Culham, 2000) con *Paspalum* y con *Panicum obtusum* Kunth [= *Hopia obstusa* (Kunth) Zuloaga & Morrone], mientras que Giussani et al. (2001) indican una estrecha afinidad de *Axonopus* con los géneros *Ophiochloa* Filg., Davidse & Zuloaga y *Streptostachys* P. Beauv., siendo esta relación más distante con los géneros *Anthaenantiopsis* Mez ex Pilg., *Echinolaena* Desv., *Ichnanthus* P. Beauv., *Ocellochloa* Zuloaga & Morrone, *Paspalum* y *Thrasya* Kunth (= *Paspalum*) y con tres especies de *Panicum* s.l. (*P. validum* Mez, *P. tuerckheimii* Hack. y *P. obtusum* [= *Hopia obtusa*]).

El estudio taxonómico más completo, efectuado hasta el momento, sobre las especies de *Axonopus* es el realizado por Black (1963, compilado por L. B. Smith). El género también ha sido tratado en diferentes estudios florísticos regionales o revisiones parciales para Argentina, sur de Brasil, Bolivia, Chile, Paraguay y Uruguay (Parodi, 1938; Rosengurtt et al., 1970; Smith et al., 1982; Tovar, 1993; Morrone et al., 1994, 1995a; Pohl & Davidse, 1994; Renvoize, 1998; Cialdella et al., 2006; Giraldo-Cañas, 2008a).

El presente trabajo tiene como objetivo contribuir al conocimiento de las especies del género *Axonopus* que crecen en la región austral de Sudamérica, incluyendo Argentina, Bolivia, sur de Brasil (Paraná, Santa Catarina, Rio Grande do Sul), Chile continental, Paraguay y Uruguay; cabe enfatizar que no se ha hallado ninguna especie de *Axonopus* en Chile continental. Se proporciona en el trabajo una clave para la identificación de las especies austro-sudamericanas, descripciones, sinonimias, distribución geográfica, observaciones e ilustraciones de las especies.

Materiales y Métodos

Los estudios morfológicos fueron realizados sobre la base de materiales pertenecientes a los siguientes herbarios: BAA, CTES, F, G, K, LIL, LPB, MBM, MO, PY, SI, US, USZ (Holmgren et al., 1990). Las disecciones fueron estudiadas con un microscopio estereoscópico Wild M5 (Widnau, Switzerland) con cámara de dibujo (SI). Las treinta y un especies estudiadas de *Axonopus* se incluyen en el Apéndice 1. Dentro del material examinado de cada especie solo se citaron ejemplares representativos de cada país; una lista completa de los especimenes estudiados, ordenados alfabéticamente por coleccionista, se presenta en el Apéndice 2.

Tratamiento Taxonómico

Axonopus P. Beauv., Ess. Agrostogr. 12. 1812. TIPO: *Axonopus aureus* P. Beauv. (lectotipo, designado por Hitchcock [1908: 142]).

Plantas perennes, rara vez anuales, cespitosas, rizomatosas o estoloníferas; cañas herbáceas o subleñosas. Vainas lateralmente comprimidas, con el dorso aquillado o redondeadas, abiertas; lígulas membranáceo-ciliadas; aurículas ausentes, o excepcionalmente presentes; láminas filiformes, lineares a linear-lanceoladas, planas a conduplicadas, raro convolutas, herbáceas a rígidas. Inflorescencias exertas, solitarias o terminales y axilares presentes, naciendo del último nudo caulinar, compuestas por racimos espiciformes, unilaterales, simples, conjugados a digitados a distribuidos a lo largo del eje principal; raquis de los racimos triquetro, cara dorsal plana, cara ventral con costilla central, escabroso o piloso, frecuentemente sinuoso; espiguillas solitarias, bi-seriadas, subsésiles a cortamente pediceladas, desarticulando por debajo de la gluma superior. Espiguillas elipsoides, ovoides a obovoides, dorsalmente comprimidas, glabras a pilosas, múticas, orientadas con el dorso de la lema inferior hacia el raquis y la gluma superior hacia afuera del raquis. Gluma inferior ausente; gluma superior y lema inferior membranáceas, subiguales, tan largas como la espiguilla, a veces ligeramente más cortas que el antecio superior, 2–9-nervias; pálea inferior y flor inferior ausentes; antecio superior endurecido, pajizo a castaño oscuro, finamente papiloso, glabro o con un mechón de pelos en el ápice; lema con márgenes levemente involutos abrazando los bordes de la pálea; lodículas 2; estambres 3; estilos 2, libres. Cariopsis con hilo elíptico o cortamente linear, subbasal; embrión 1/3–1/2 de la longitud de la cariopsis.

Número básico de cromosomas. $x = 10$ (Watson & Dallwitz, 1992: 150).

Anatomía foliar. Las especies del género *Axonopus* son uniformemente C_4 Kranz del subtipo MS,

NADP-me (Brown, 1977; Hattersley & Watson, 1992); este subtipo anatómico está caracterizado por incluir una única vaina mestomática alrededor de los haces vasculares, la que lleva cloroplastos especializados.

Hábitat y distribución. *Axonopus* es un género con aproximadamente 85 especies distribuidas en regiones tropicales y subtropicales del Nuevo Mundo, con unas pocas especies que crecen en el Viejo Mundo. En el sur de América del Sur habitan 31 especies desde el nivel del mar hasta los 3000 m.s.n.m.

En América *Axonopus* se extiende desde el Sur de los Estados Unidos de América hasta Uruguay y Argentina (Black, 1963; Cialdella et al., 2006), presentando una mayor concentración de especies en el norte de Sudamérica, en Venezuela, Surinam, Guyana, Guayana Francesa, Colombia y Brasil (Giraldo-Cañas, 1999, 2000). Desde el punto de su importancia económica, varias especies son utilizadas como forrajeras naturales como por ejemplo: *A. compressus* (Sw.) P. Beauv., *A. fissifolius* (Raddi) Kuhlm., *A. purpusii* (Mez) Chase, *A. scoparius* (Flüggé) Kuhlm. y *A. suffultus* (J. C. Mikan ex Trin.) Parodi. *Axonopus compressus* también es apreciada como césped (carpet grass; Black, 1963; Nicora & Rúgolo de Agrasar, 1987).

Clave para Distinguir las Especies de *Axonopus* de Sudamérica Austral

1. Raquis fuertemente papiloso-piloso en toda su extensión, pelos de base tuberculada de hasta de 4 mm 2
1. Raquis glabro o solamente piloso junto a la inserción de los pedicelos, pelos simples, no mayores de 2 mm..... 5
2(1). Espiguillas glabras a glabrescentes; raquis con pelos dorados; antecio superior glabro..... 3
2. Espiguillas con la gluma superior y lema inferior densamente híspidas, con pelos papilosos; raquis con pelos blanquecinos o dorados; ápice del antecio superior con un mechón de pelos blanquecinos 4
3(2). Espiguillas dispuestas en cavidades cupuliformes sobre el raquis; raquis de 1–1.5 mm de ancho, terminando en una prolongación estéril..... 8. *A. chrysoblepharis*
3. Espiguillas dispuestas libremente a lo largo del raquis, no hundidas en cavidades cupuliformes; raquis de 0.4–0.8 mm de ancho, terminando en una espiguilla desarrollada ..... 3. *A. aureus*
4(2). Vainas basales flabeladas, láminas de ápice redondeado, raquis con pelos rígidos, dorados, con mayor densidad asociada a la base del pedicelo ..... 15. *A. herzogii*
4. Vainas basales no flabeladas, láminas de ápice agudo, raquis con pelos sedosos, blanquecinos, distribuidos homogéneamente ..... 5. *A. brasiliensis*
5(1). Gluma superior y lema inferior con nervios marcados, surcadas a levemente cóncavas entre los nervios, con el nervio medio usualmente presente 6
5. Gluma superior y lema inferior con nervios no marcados, lisas, con el nervio medio ausente o excepcionalmente presente, pero no conspicuo..... 15
6(5). Espiguillas de 3.6–5 mm..... 7
6. Espiguillas menores de 3.6 mm..... 8
7(6). Espiguillas glabras a esparcidamente pilosas, con unos pocos pelitos dispersos entre los nervios; láminas filiformes, macizas, de 0.3–1.2 mm de ancho; nudos glabros a esparcidamente pilosos..... 9. *A. comans*
7. Espiguillas hispidas, con largos pelos blanquecinos hasta de 2.4 mm, distribuidos en la base y a lo largo de los márgenes; láminas lineares, conduplicadas a involutas, de 2–5 mm de ancho; nudos vilosos..... 31. *A. uninodis*
8(6). Antecio superior castaño oscuro en la madurez, 0.6–0.8 mm menor que la gluma superior y lema inferior..... 19. *A. leptostachyus*
8. Antecio superior pajizo, igual o hasta 0.4 mm menor que la gluma superior y la lema inferior..... 9
9(8). Plantas con cañas comprimidas; láminas lanceoladas, planas, de 0.5–3.9 cm de ancho, ápice de las láminas agudo a obtuso 10
9. Plantas con cañas cilíndricas, ocasionalmente comprimidas en *A. andinus*; láminas filiformes o largamente lineares, no mayores de 1.2 cm de ancho, ápice de las láminas acuminado, pungente o filamentoso 12
10(9). Base de las plantas iridácea; láminas de 5–32 × 0.5–1.2 cm; inflorescencias con 4–7 racimos; nudos barbados ..... 12. *A. equitans*
10. Base de las plantas no iridácea; láminas de 6–50 × 0.5–4 cm; inflorescencias con 6–100 o más racimos; nudos glabros a pubescentes... 11
11(10). Plantas de 50–120 cm de alto; inflorescencias con 6–20 racimos, racimos secundarios ausentes..... 17. *A. iridifolius*
11. Plantas de 70–200 cm de alto; inflorescencias con 10–100 o más racimos, secundarios usualmente presentes ..... 27. *A. scoparius*
12(9). Plantas con las vainas densamente vilosas, con pelos de color plateado..... 22. *A. pellitus*
12. Plantas con las vainas glabras o esparcidamente pilosas, sin pelos largos plateados..... 13
13(12). Vainas densamente superpuestas en región media y apical de la caña; láminas plegadas, falcadas, de ápice agudo a subagudo ..... 7. *A. caulescens*
13. Vainas predominantemente basales o distribuidas por toda la caña; láminas filiformes o planas, no falcadas, de ápice acuminado o largamente agudo..... 14
14(13). Plantas gráciles no mayores de 1 m de alto; láminas linear-lanceoladas a lanceoladas y de ápice acuminado; inflorescencia con 5–8 racimos ..... 1. *A. andinus*
14. Plantas robustas hasta de 2.3 m de alto; láminas filiformes a lineares, de ápice pungente; inflorescencias con (3–)7–60 ramificaciones..... 28. *A. siccus*
15(5). Antecio superior castaño a la madurez 16

15. Antecio superior pajizo a blanquecino a la madurez 23
16(15). Plantas anuales; espiguillas de 0.9–1.3(–1.5) mm; inflorescencias de 1.4–5 cm, láminas lanceoladas, de base subcordada, distinguible de la vaina ..... 6. *A. capillaris*
16. Plantas perennes; espiguillas de (1.3–)1.7–3 mm; inflorescencias de (6–)8–32 cm; láminas lineares a linear-lanceoladas, de base angosta, continuándose imperceptiblemente con la vaina, o redondeada con aurículas 17
17(16). Espiguillas con los márgenes de la gluma superior pestañosos, con pelos pectinados tuberculados, blanquecinos hasta de 0.8 mm ..... 18. *A. kuhlmannii*
17. Espiguillas glabras o pubescentes, con pelos delicados, distribuidos entre los espacios internervales 18
18(17). Vainas basales conspicuamente dísticas, equitantes; plantas lateralmente comprimidas, de aspecto iridáceo 19
18. Vainas basales dispuestas alrededor de las cañas, no dísticas; planas no lateralmente comprimidas, de aspecto no iridáceo 20
19(18). Plantas con vainas generalmente glaucas con zonas violáceas, rara vez pajiza; láminas predominantemente basales; gluma superior de 1.9–2.5 mm, igual o levemente mayor que el antecio superior; sur de Brasil, Uruguay, Paraguay y noreste y centro de Argentina ..... 30. *A. suffultus*
19. Plantas con vainas pajizas, glabras a vilosas, nunca glaucas; láminas dispuestas hasta la porción media de las cañas; gluma superior 1.2–1.5(–2.2) mm, generalmente menor que el antecio superior; Bolivia, Guyana, Guayana Francesa, Surinam, Venezuela ..... 14. *A. flabelliformis*
20(18). Vainas con aurículas; láminas de 30–52 × 1–2 cm ..... 29. *A. succulentus*
20. Vainas sin aurículas; láminas de 5–45 × 0.2–2 cm 21
21(20). Plantas cespitosas; espiguillas de 2–3 mm; plantas generalmente robustas; nudos glabros ... 22
21. Plantas estoloníferas; espiguillas de (1.5–)1.7–2 mm; plantas grráciles; nudos densamente pilosos ..... 11. *A. cuatrecasasii*
22(21). Plantas con rizomas estoloníferos, falciformes o rectos, cilíndricos, de entrenudos largos, cubiertos de numerosos catáfilos coriáceos, con el dorso redondeado; láminas de 2–7 mm de ancho ..... 2. *A. argentinus*
22. Plantas con rizomas cortos, gruesos, comprimidos lateralmente, de entrenudos cortos, cubiertos por catáfilos rígidos; láminas de 5–20 mm de ancho ..... 24. *A. pressus*
23(15). Espiguillas insertas oblicuamente en los pedicelos ..... 25. *A. purpusii*
23. Espiguillas insertas horizontalmente en los pedicelos 24
24(23). Espiguillas híspidas, con pelos firmes, rígidos, blanco-plateados, purpúreos o fuscescentes, hasta de 2 mm .... 20. *A. marginatus*
24. Espiguillas glabras a esparcidamente pilosas, con pelos suaves, blanquecinos, cortos, hasta de 0.7 mm 25
25(24). Inflorescencias con 3–20 racimos; plantas cespitosas; vainas basales de aspecto iridáceo ..... 23. *A. polystachyus*
25. Inflorescencias con 2(o 3–4) racimos; plantas estoloníferas, vainas basales no iridáceas 26
26(25). Espiguillas de (3.2–)3.4–5.5 mm 27
26. Espiguillas de 1.5–2.6(–3) mm 28
27(26). Racimos distanciados entre sí; láminas lanceoladas, con prefoliación convoluta, de 1–2.3 cm de ancho ..... 21. *A. obtusifolius*
27. Racimos aproximados a subconjugados; láminas linear-lanceoladas, con prefoliación conduplicada, de 0.5–1 cm de ancho ..... 26. *A. rosengurttii*
28(26). Láminas glabras a esparcidamente pilosas en ambas caras, los márgenes glabros, en ocasiones pestañosos hacia la porción basal 29
28. Láminas densamente pilosas en ambas caras, con pelos de base tuberculada, los márgenes pestañosos 30
29(28). Láminas linear-lanceoladas a lanceoladas, con prefoliación convoluta, de 0.5–1.2 cm de ancho, de base subcordada; espiguillas ovoides, de 0.8–1.2 mm de ancho; antecio superior 0.4–0.8 mm menor que la gluma superior y la lema inferior ..... 10. *A. compressus*
29. Láminas lineares, con prefoliación conduplicada, de 0.2–0.4(–0.5) cm de ancho, de base angosta, continuándose imperceptiblemente con la vaina; espiguillas elipsoides de 0.4–0.6 mm de ancho; antecio superior igual o hasta de 0.3 mm menor que la gluma superior y lema inferior ..... 13. *A. fissifolius*
30(28). Plantas anuales; nudos glabros; antecio superior glabro ..... 4. *A. boliviensis*
30. Plantas perennes; nudos barbados; antecio superior con un mechón de pelos en el ápice ..... 16. *A. hirsutus*

1. Axonopus andinus G. A. Black, Advancing Frontiers Pl. Sci. 5: 111. 1963. TIPO: Bolivia. La Paz: Hac. Simaco sobre el camino a Tipuani, 1400 m, feb. [abr. en protólogo] 1920, *Otto Buchtien 5328* (holotipo, US 1164712!; isotipos, MO 941455!, MO fragm. en SI!, US 1099092!, US fragm. en SI!). Figura 1.

Plantas perennes, rizomatosas, de 50–100 cm de alto; cañas erectas a geniculadas, delgadas, comprimidas, de 1.5–1.8 cm diám., pajizas o con tintes violáceos, longitudinalmente estriadas; entrenudos 3–6, los superiores hasta de 8 cm; nudos castaños, glabros. Vainas de 2–9 cm, distribuidas uniformemente a lo largo de la caña, glabras, estriadas, los márgenes membranáceos, glabros o pestañosos hacia la porción superior; lígulas membranáceo-ciliadas, de 0.4–0.5 mm; cuello distinguible, castaño, glabro; láminas linear-lanceoladas a lanceoladas, de 3–15 × 0.5–1 cm, planas, glabras o esparcidamente pilosa en la base, ápice acuminado y base subcordada, los márgenes escabriúsculos, pestañosos hacia la base y

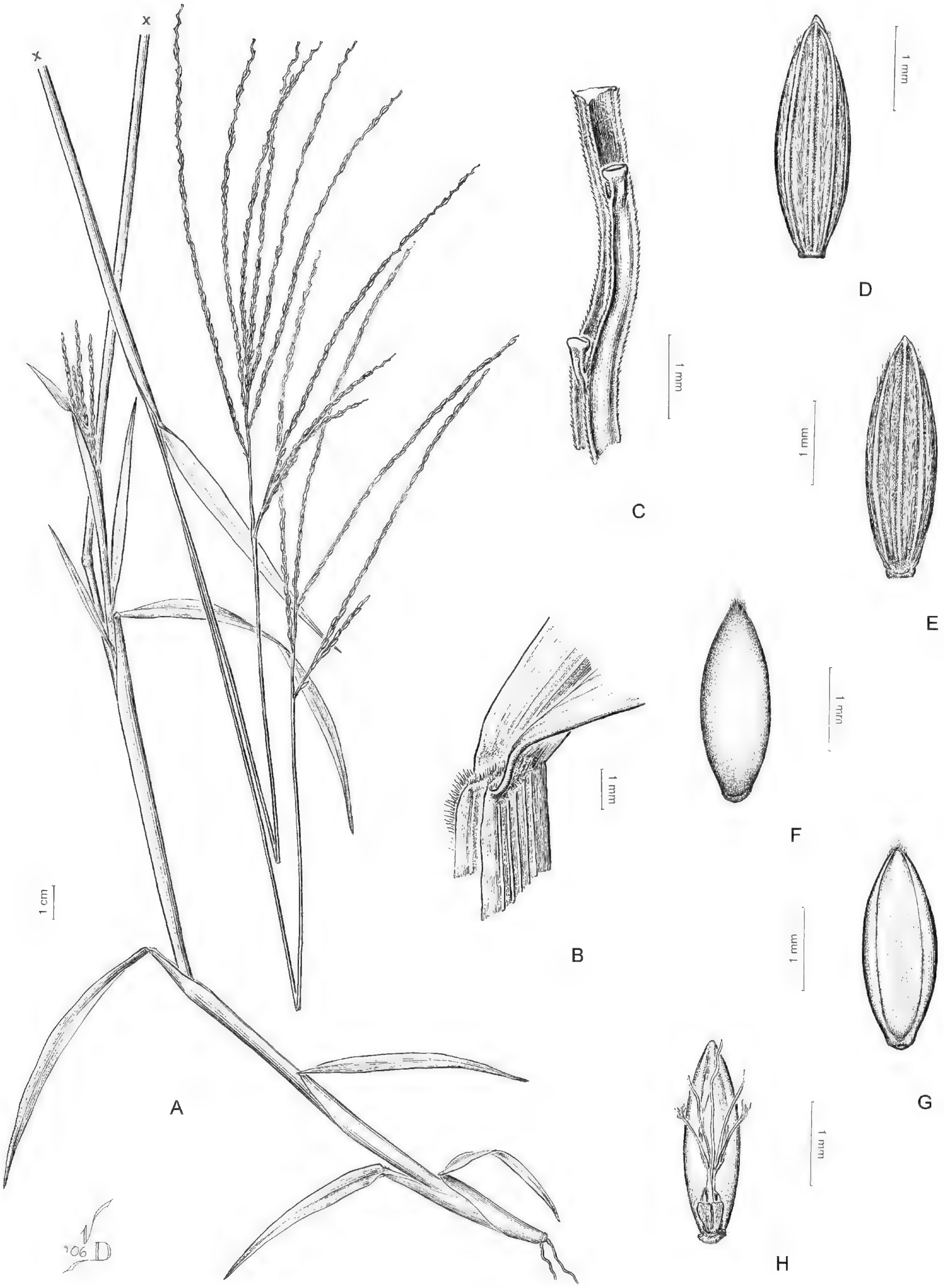


Figura 1. *Axonopus andinus* G. A. Black. —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Espiguilla, vista del lado de la gluma superior. —E. Espiguilla, vista del lado de la lema inferior. —F. Antecio superior, vista dorsal mostrando la lema superior. —G. Antecio superior, vista ventral mostrando la pálea superior. —H. Pálea superior, lodículas y filamentos estaminales (*López et al. 386*, LPB).

luego glabros. Inflorescencias terminales, de 5–13 × 1.5–3 cm; pedúnculos 1 o 2, de 25–40 cm, filiformes, con un surco lateral conspicuo, glabro; eje principal anguloso, de 25–40 × 0.4–0.6 mm, con 5–8 racimos, ascendentes, divergentes, alternos, los superiores conjugados; raquis triquetro, de 50–100 × 0.4–0.5 mm, glabro o con algunos pelos aislados, los márgenes escabriúsculos; pedicelos cortos de 0.4–0.5 mm, glabros, escabriúsculos. Espiguillas elipsoides, de 2.4–2.6 × 0.7–0.8 mm, glabras, o cortamente pilosas a lo largo de los nervios, de ápice agudo, pajizas o con tintes violáceos; gluma superior y lema inferior subiguales, tan largas como el antecio superior; gluma superior de 2.2–2.5 mm, membranácea-hialina, glabra o con algunos pelos ralos, 2–4(5)-nervia; lema inferior glumiforme, 2(3)–4-nervia; antecio superior elipsoide, de 2.1–2.3 × 0.6–0.8 mm, pajizo, finamente papiloso en toda su superficie, de ápice subagudo y con un pequeño mecho de pelos blanquecinos; pálea superior similar en textura y ornamentación a la lema, glabra; lodículas 2, ca. 0.2 mm; estambres 3, anteras de 1.2–1.5 mm, purpúreas. Cariopsis no visto.

Hábitat y distribución. *Axonopus andinus* es una especie endémica de Bolivia, coleccionada hasta el presente en el Departamento de La Paz en bordes de bosques, en lugares sombríos, entre los 900 y 1900 m.s.n.m.

Discusión. Esta especie es morfológicamente afín a *Axonopus scoparius*, distinguiéndose esta última por su hábito más robusto, con cañas de 0.7–2 m de alto (vs. 0.5–1 m en *A. andinus*), láminas lanceoladas, de 15–50 × 0.7–4 cm (vs. linear-lanceoladas a lanceoladas, de 3–15 × 0.5–1 cm) y inflorescencias de 12–35 cm de largo, con 10 a más de 100 racimos (vs. 5–13 cm de largo, con 5–8 racimos).

Black (1963) incluyó a *Axonopus andinus* bajo la clave de las especies de la serie *Axonopus* P. Beauv. y en la clave y en el tratamiento de *Axonopus* ser. *Barbigeri*. El análisis de los ejemplares tipos de *A. andinus* y de dos ejemplares de herbario permitió determinar que la mayoría de las espiguillas poseen la gluma superior y la lema inferior con el nervio medio y los laterales conspicuos, carácter que es propio de las especies de la serie *Barbigeri*, aunque en algunas espiguillas el nervio medio puede estar ausente.

En la descripción original Black (1963) indica que el ejemplar tipo fue coleccionado en el mes de abril. El análisis del material tipo permitió verificar que el mismo fue coleccionado en el mes de febrero de 1920.

Material adicional examinado. BOLIVIA. **La Paz:** Murillo, valle del Río Zongo, *Solomon 18850* (LPB, MO, SI), valle del Río Zongo, entre Cahua y Huaji, *López et al. 386* (LPB), Zongo Valley, *Renvoize et al. 4263* (LPB, MO); Nor Yungas, 16.5 km NO de Chuspipata por el camino a Yolosa, *Solomon 18509* (LPB), Camino de Tolosa a La Paz, *Morrone & Belgrano 4904* (SI).

2. Axonopus argentinus Parodi, Notas Mus. La Plata, Bot. 3(17): 15, fig. 1. 1938. *Axonopus argentinus* var. *genuinus* Parodi, Notas Mus. La Plata, Bot. 3: 15. 1938, nom. inval. TIPO: Argentina. Entre Ríos: Concordia, hab. campo ca. de la Est. Agronomía, 22 ene. 1922, *L. R. Parodi 4649* (holotipo, BAA 300!; isotipos, IAN no visto, SI!, US 1723532!, US foto en SI!).

Axonopus argentinus var. *glabriflorus* Parodi, Notas Mus. La Plata, Bot. 3(17): 19. 1938. TIPO: Uruguay. Salto, ene. 1937, *G. Orihuela 60, Hb., Mus. Nac. Montevideo 5038* (holotipo, BAA 302!; isotipos, MVM no visto, US 2236050!, US fragm. ex BAA!).

Axonopus argentinus var. *glabripes* Parodi, Notas Mus. La Plata, Bot. 3(17): 19. 1938. *Axonopus argentinus* subsp. *glabripes* (Parodi) Roseng., B. R. Arrill. & Izag., Gram. Urug. 293, f. 21. 1970. TIPO: Argentina. Entre Ríos: Dpto. Concordia, Pedermar [sic, Pedernal], mayo 1933, *J. Friedermann 60* (holotipo, BAA 303!; isotipo, IAN no visto).

Axonopus argentinus f. *hirsutus* Parodi, Notas Mus. La Plata, Bot. 3(17): 18. 1938. TIPO: Argentina. Entre Ríos: Dpto. Concordia, Concordia, feb. 1930, *L. R. Parodi 9584* (holotipo, BAA 305!; isotipo, IAN no visto).

Axonopus suffultus (J. C. Mikan ex Trin.) Parodi var. *pubiflorus* Parodi, Notas Mus. La Plata, Bot. 3(17): 23. 1938. *Axonopus argentinus* subsp. *pubiflorus* (Parodi) Roseng., B. R. Arrill. & Izag., Gram. Urug. 293. 1970. TIPO: Uruguay. Montevideo: Sayago, 22 dic. 1921, *L. R. Parodi 91* (holotipo, BAA 334!; isotipos, IAN no visto, SI!, US 1127741!, US foto en SI!).

Axonopus hagenbeckianus (Kuntze) Parodi var. *pratensis* G. A. Black, Advancing Frontiers Pl. Sci. 5: 141. 1963. TIPO: Brasil. Rio Grande do Sul: Porto Alegre, Morro da Gloria, 26 oct. 1945, *B. Rambo 29313* (holotipo, US 1910224!; isotipo, LIL no visto, US foto en SI!).

Axonopus ramboi G. A. Black, Advancing Frontiers Pl. Sci. 5: 134. 1963. TIPO: Brasil. Rio Grande do Sul: Cambará, 29°S, 50°W, in dumetis, 30 ene. 1948, *B. Rambo 36460* (holotipo, US 1935537!; isotipo, K!, US foto en SI!).

Axonopus paraguayensis G. A. Black, Advancing Frontiers Pl. Sci. 5: 135. 1963. TIPO: Paraguay. Caapucú, Est. Barrerito, campo orillas montes, ene. 1949, *T. Rojas 13103a* (holotipo, US 2012988!, US foto en SI!; isotipo, K!).

Plantas perennes, cespitosas, con rizomas delgados, estoloníferos, falciformes, cubiertos por numerosos catáfilos coriáceos; cañas erectas, de 20–100 cm de alto, 2–5 mm diám., comprimidas; entrenudos 2–4, de 2.5–20 cm, con uno de los lados surcado, longitudinalmente estriados, pajizos, glabros o con pelos cortos sobre el surco lateral y hacia la porción

superior; nudos glabros, castaños. Vainas predominantemente basales, de 4–15 cm, generalmente mayores que los entrenudos, glabras a densamente vilosas sobre todo hacia la parte superior, aquilladas, estriadas; las vainas superiores hasta de 27 cm; lígulas membranáceo-ciliadas, de 0.4–1 mm, porción superior con pelos densos y blanquecinos; cuello distinguible, castaño, glabro a piloso; láminas lineares, de 8–36(–40) × 0.2–0.7 cm, conduplicadas en la base y planas hacia el ápice, estriadas, glabras o con escasos pelos sobre el nervio medio en la cara adaxial, de base angosta continuándose imperceptiblemente con la vaina, ápice obtuso a subagudo, los márgenes escabriúsculos u ocasionalmente pestañosos hacia la región basal. Inflorescencias terminales y axilares en el último nudo caulinar, de 8–17 × 2–6 cm, exertas; 2 o 3 pedúnculos, de 28–50 cm, aplanados, con un lado surcado, glabros; eje principal anguloso, de 2–6 × 0.7–0.9 mm, escabríusculo en los márgenes; racimos 3–15(–20), ascendentes, divergentes, alternas, los superiores aproximados; raquis de los racimos triquetro, de 80–180 × 0.6–0.7 mm, ondulado, híspídulo, con los márgenes escabriúsculos, generalmente con 2–6 pelos situados sobre los ángulos a ambos lados de la base de cada pedicelo, pelos de 1–2 mm, blanquecinos; pulvínulos pilosos; pedicelos de 0.2–0.3 mm, aplanados, glabros u ocasionalmente con algún pelo similar a los del raquis. Espiguillas elipsoides de 1.9–3 × 0.6–1 mm, glabras a cortamente pilosas entre los nervios, de ápice agudo a subagudo, pajizas o con tintes violáceos; gluma inferior y lema superior subiguales, tan largas como el antecio superior o hasta de 0.6 mm mayores; gluma superior de 1.9–3 mm, membranáceo-hialina, 2(–4)-nervia, el nervio medio ausente; lema inferior glumiforme, 2(–4)-nervia; antecio superior elipsoide, de 1.8–2.4 × 0.6–0.7 mm, castaño en el dorso y en ocasiones pajizo en el ápice y en la base, finamente papiloso en toda la superficie, de ápice obtuso, glabro; pálea similar en textura y ornamentación a la lema, glabra; lodículas 2, ca. 0.3 mm, membranáceas, conduplicadas; estambres 3, anteras de 1–1.5 mm. Cariopsis elipsoide, de 1.5 × 0.6 mm, blanquecina; hilo oblongo, embrión 1/2 del largo de la cariopsis.

Hábitat y distribución. *Axonopus argentinus* crece en el sudeste y sur de Brasil (Paraná, Rio Grande do Sul y Santa Catarina), Paraguay (en la región oriental y occidental), Uruguay (Artigas, Canelones, Cerro Largo, Durazno, Flores, Florida, Lavalleja, Montevideo, Paysandú, Salto, San José y Tacuarembó) y la Argentina (Chaco, Corrientes, Entre Ríos, Misiones y Santa Fe). Esta especie es común en bordes de montes, campos semihúmedos o en suelos arenosos-rocosos más secos, desde el nivel del mar hasta los 500 m.s.n.m.

Nombre vulgar. "Kapi'ipe ñu" (Paraguay, Morrone et al., 1994: 29).

Número cromosómico. Se ha citado para *Axonopus argentinus* un recuento cromosómico de $n = 20$ (Hickenbick et al., 1975: 189, sub *A. ramboi* G. A. Black).

Discusión. *Axonopus argentinus* pertenece a la serie *Suffulti* G. A. Black, y es morfológicamente afín a *A. suffultus* y *A. pressus* (Nees ex Steud.) Parodi. *Axonopus suffultus* se distingue de *A. argentinus* por tener rizomas con entrenudos cortos, no viajeros (vs. estoloníferos, viajeros), vainas glaucas y cuello indistinguible. *Axonopus pressus* se diferencia de *A. argentinus* por ser plantas más robustas, hasta de 150 cm de alto (vs. hasta de 100 cm de alto en *A. argentinus*) y con gruesas innovaciones comprimidas, cubiertas por vainas dísticas (vs. innovaciones delgadas, no comprimidas, no cubiertas por vainas dísticas) y láminas linear-lanceoladas, rígidas y frecuentemente bipartidas en el ápice (vs. láminas lineares, obtusas a subagudas y de ápice entero en *A. argentinus*). *Axonopus pressus* posee asimismo inflorescencias hasta de 32 cm, con 26 a 34 racimos por inflorescencia (vs. inflorescencias hasta de 17 cm y con 3 a 15 [hasta 20] racimos por inflorescencia en *A. argentinus*). Para una mayor aclaración de la variación morfológica y sinonimia véase Cialdella et al. (2006).

Material adicional examinado. ARGENTINA. **Chaco:** Dpto. 1° de Mayo, Colonia Benítez, *Schulz 11786* (BAA, CTES, F, MO). **Corrientes:** Dpto. Capital, Riachuelo, *Schinini & Ahumada 12361* (CTES, F, SI). **Entre Ríos:** Dpto. Uruguay, Concepción del Uruguay, Est. Río Uruguay, ca. Gualeguaychú, *Burkart 24078* (BAA, SI). **Misiones:** Dpto. Capital, Posadas, Establ. Santa Inés, *Parodi 4632* (BAA). **Santa Fe:** Dpto. General Obligado, Camino de Reconquista a Dr. Barros Pasos, *Job 760* (BAA, F). BRASIL. **Paraná:** São Cristobal, Mun. Unizo da Victoria, *Hatschbach 30691* (MBM). **Rio Grande do Sul:** Uruguaiana, *Swallen 7638* (MO, US). **Santa Catarina:** Mun. Lajes, Lajes, *Swallen 8110* (MO, US). PARAGUAY. Tuyutí, *Eskuche 2528-8* (SI). **Alto Paraná:** Puerto Casado, *Ramírez 649* (US). **Amambay:** Pedro Juan Caballero, Sierra de Amambay, *Rojas 6704* (BAA). **Central:** San Lorenzo del Campo Grande, Escuela Mariscal Estigarribia, *Rojas 14105* (LIL, US). **Cordillera:** Ea. Barrerito, Caapucú, *Rojas 13129* (BAA, CTES, LIL). **Guairá:** Iturbe, *Montes 12834* (BAA, CTES). **Misiones:** Santiago, La Soledad, *Pedersen 9600* (CTES). **Paraguarí:** Cerro Corá, près de Paraguarí, *Balansa 97* (G, MO). URUGUAY. **Artigas:** Puente Bella Unbión, Río Cuareim, *Rosengurtt B-7406* (F). **Canelones:** 1° de Mayo, Parque Centenario, *Rosa-Mato 1463* (BAA). **Cerro Largo:** Río Negro, entre Losayos Palleros y Areguá, *Rosengurtt 1063* (BAA, US). **Durazno:** Maestre Campo, *Dauber 111* (BAA). **Flores:** Río Jí, *Rosengurtt B-588* (BAA,

US). **Florida:** Timote, Santa Clara, San José, *Gallinal et al. 2907* (F, US). **Lavalleja:** Ea. Pororó, *Pedersen 3638* (BAA, CTES). **Montevideo:** Montevideo, *Arechavaleta s.n.* (BAA-301, SI). **Paysandú:** Costa del Río Uruguay, *Lombardo 3032* (BAA). **Salto:** Río Uruguay y Ayo. San Antonio Grande, *Rosengurtt B-955* (BAA). **Tacuarembó:** Ruta 5, Km 399, Ayo. Tres Cruces, *Seijo et al. 2528* (CTES, SI).

3. Axonopus aureus P. Beauv., Ess. Agrostogr. 12. 1812. TIPO: Guayana Francesa. Savanne Corossony, PK 111 de la route Cayenne–St. Laurent, 27 dic. 1986, *G. Cremers 9571* (neotipo, designado por Garófalo-Spalding [1990: 88], US 3131005!; isotipos, B no visto, BR no visto, CAY no visto, INPA no visto, MG no visto, MO 3524121!, MO foto en SI!, NY!, P no visto, PORT no visto, U no visto, VEN!).

Paspalum canescens Nees ex Trin., Gram. Panic. [Trinius]: 89. 1826. *Axonopus canescens* (Nees ex Trin.) Pilg. in Engl. & Prantl, Nat. Pflanzenfam., ed. 2. [Engler & Prantl], 14E: 55. 1940. TIPO: Brasil. s. loc., s.d., *G. H. von Langsdorff s.n.* (holotipo, LE TRIN 0634.01!; isotipos, B no visto, B fragm. en US 2942166!, K no visto, LE fragm. en SI!, LE fragm. en US 2942166!).

Paspalum pulchrum Nees, Fl. Bras. Enum. Pl. 2(1): 79. 1829, como "*Paspalus pulcher*". *Panicum pulchrum* Willd. ex Spreng., Syst. Veg. (ed. 16) [Sprengel] 1: 272. 1824, pro syn., nom. nud. *Axonopus pulcher* (Nees) Kuhlm., Relat. Comiss. Linhas Telegr. Estratég. Matto Grosso Amazonas 67(11): 88. 1922. TIPO: América del Sur, s.d., *F. W. H. A. Humboldt s.n.* (lectotipo, designado por Garófalo-Spalding [1990: 89], B!; isotipo, BM!).

Paspalum exasperatum Nees, Fl. Bras. Enum. Pl. 2(1): 81. 1829, como "*Paspalus exasperatus*", nom. illeg. superfl., sub *Cabrera chrysoblepharis* Lag. *Axonopus exasperatus* (Nees) G. A. Black, Advancing Frontiers Pl. Sci. 5: 168, f. 8d. 1963, nom. illeg. TIPO: Brasil. Bahia: "Ad margines sylvarum prope Ferradas prov. Bahiensis, in via Felisbertiana, quae decendit e Minis. Dec.", *K. F. P. von Martius s.n.* (holotipo, M no visto; isotipos, LE TRIN 0452.01!, M fragm. en US 2941994!, P!).

Panicum chrysites Steud., Syn. Pl. Glumac. 1: 38. 1853. *Axonopus chrysites* (Steud.) Kuhlm., Relat. Comiss. Linhas Telegr. Estratég. Matto Grosso Amazonas 67(11): 88. 1922. TIPO: Guayana Francesa. 1838, *M. Leprieur s.n.* (holotipo, P no visto; isotipos, MO 1640149!, MO foto en SI!, US 2305567!, US fragm. en SI!).

Plantas perennes, cespitosas, cortamente rizomatosas; cañas erectas o en ocasiones decumbentes, arraigadas en los nudos basales, de 30–120 cm, 1–2.5 mm diám., cilíndricas en la base a comprimidas en el ápice; entrenudos 3–10, de 1.2–15 cm, ocasionalmente surcados, pajizos, glabros; nudos gabros, castaño oscuros a negruzcos. Vainas distribuidas uniformemente a lo largo de las cañas o más raramente basales, de 2–14 cm, glabras o en ocasiones pubescentes hacia la porción superior, aquilladas, con los márgenes membranáceos o pestañosos hacia la región superior; lígulas membranáceo-ciliadas, de 0.2–0.8 mm, con pelos blanquecinos y brillantes; cuello indistinguible o distinguible, glabro o con pelos cortos y blanquecinos; láminas linear a linear-lanceoladas, de 3–32 × 0.2–1 cm, planas a conduplicadas, estriadas, glabras a pubescentes o pilosas hacia la región ligular sobre la cara adaxial, de base generalmente angostada en la zona de unión con la vaina, el ápice agudo a largamente acuminado, los márgenes escabriúsculos, pestañosos hacia la región basal, con pelos tuberculados, blanquecinos hasta de 4 mm. Inflorescencias terminales o axilares, de 3–16 × 1–4 cm, exertas; 1 o 2 pedúnculos naciendo del último nudo caulinar, de 12–40 cm, cilíndricos, lisos, glabros o pilosos en la región apical, con pelos dorados, de base tuberculada; pulvínulos pilosos; eje principal anguloso, de 0–30 × 0.5–0.7 mm, hirsuto, con pelos tuberculados, dorados; racimos 2–14, ascendentes, divergentes, alternos o aproximados; raquis de los racimos triquetro, de 30–120 × 0.4–0.8 mm, de márgenes pestañosos, con pelos tuberculados, dorados; pedicelos hasta de 0.2 mm, con 5–15 pelos rígidos, tuberculados, dorados, dispuestos más densamente hacia la base. Espiguillas elipsoides a obovoides, de 1.1–2.2 × 0.5–0.8 mm, pajizas a castañas, glabras o esparcidamente pilosas, con pelos cortos, blanquecinos distribuidos a lo largo de los espacios internervales, de ápice obtuso a agudo; gluma superior de 1.1–2.2 mm, hialina, 2(o 3)-nervia, en ocasiones el nervio medio presente; lema inferior glumiforme, 2(o 3)-nervia; antecio superior elipsoide u obovoide, de 1.1–2.1 × 0.5–0.8 mm, castaño oscuro, ocasionalmente con el ápice y la base pajizos, glabro, finamente papiloso, de ápice obtuso; pálea de textura y ornamentación similar a la lema; lodículas 2, ca. 0.2 mm, membranáceas; estambres 3, anteras de 0.6–1 mm, purpúreas. Cariopsis elipsoide a obovoide, de 0.9–1.4 × 0.5–0.7 mm, castaña a purpúrea; hilo elíptico; embrión 1/3–1/2 del largo de la cariopsis.

Hábitat y distribución. Esta especie posee una distribución amplia; se la encuentra desde Mesoamérica hasta Bolivia (Beni, La Paz, Santa Cruz) y sur de Brasil (Paraná y São Paulo, Valls et al., 2001: 132). *Axonopus aureus* crece en campos o sabanas entre los 150 y 2150 m.s.n.m.

Nombres vulgares. "Rabo de rapoza", "Capim perdiz", "Capim de cerrado", "Capim ourihno", "Paja cienpies", "cola de Burro, "Paja peluda",

"Paja de Canta", "Pata de Pava" (Giraldo-Cañas, 2001: 216).

Número cromosómico. Existe para *Axonopus aureus* un único recuento, citada como diploide, $2n = 20$ (Pohl & Davidse, 1971: 299, sub *A. aureus* P. Beauv.).

Discusión. *Axonopus aureus*, miembro de la sección *Cabrera* (Lag.) Chase, se distingue facilmente por su raquis triquetro, con pelos dorados de base tuberculada, espiguillas glabras dispuestas libremente a lo largo del raquis y antecio superior castaño oscuro. Esta especie es morfológicamente afín a *A. chrysoblepharis* (Lag.) Chase, la que se distingue principalmente por tener las espiguillas alojadas en cavidades cupuliformes del raquis y raquis más ancho, de 1–1.5 mm (vs. 0.5–0.7 mm), terminando su ápice en una prolongación estéril.

Al describir *Paspalum exasperatum*, Nees (1829) cita erróneamente bajo la sinonimia a *Cabrera chrysoblepharis* Lag., siendo este último nombre el basiónimo de *Axonopus chrysoblepharis* (Lag.) Chase. De acuerdo al ICBN (McNeill et al., 2006: Art. 52), *Paspalum exasperatum* es un nombre superfluo ilegítimo. El material tipo citado por Nees bajo *Paspalum exasperatum* es *A. aureus* y no *A. chrysoblepharis*; por esta razón se incluye a *Paspalum exasperatum* bajo la sinonimia de *A. aureus*.

Black (1963) considera a *Axonopus exasperatus* como un taxón válido e incluye bajo la sinonimia a *Panicum exasperatum* Nees ex Steud. Steudel (1853: 62) trata a *Panicum exasperatum* bajo *Panicum* sect. *Brachiaria* Trin. De acuerdo al protólogo el tipo de *Panicum exasperatum* fue coleccionado en Guinea y posee "...spiculis geminis..., caryopsi grosee transversim rugosa longe mucronata lutescens"; el hecho de poseer el tipo antecio transversalmente rugoso indica que este taxón no debe considerarse en *Axonopus*, dado que este último género tiene antecio superior uniformemente liso.

Giraldo-Cañas (2001) trata a *Axonopus canescens* y *A. exasperatus* como sinónimos de *A. aureus* y considera a este último taxón como una entidad polimorfa en donde los extremos de variación, que anteriomente fueron interpretados como nuevos taxones, corresponden a variantes locales. El análisis de abundante material de herbario permitió confirmar lo expuesto por Giraldo-Cañas (2001), observándose una marcada variación continua en los caracteres morfológicos que no permiten separar entidades discretas.

Material adicional examinado. BOLIVIA. **Beni:** Prov. Ballivián, Espíritu, en la zona de influencia del Río Yacuma, *Beck 3374* (CTES, LPB, MO). **La Paz:** Tamayo, Apolo, 57 km hacia Charasani pasando Correo, Camp. Calabatea, *Beck 18510* (K, LPB, MO, SI). **Santa Cruz:** Ñuflo de Chávez, Ea. Viera, 2 km SE of Concepción, *Killeen 1629* (CTES, F, LPB, MO). BRASIL. **Paraná:** Mun. Rio Branco do Sul, Serra Bromado, *Hatschbach 44552* (CTES, F, MO).

4. Axonopus boliviensis Renvoize, Gram. Bolivia 496. 1998. TIPO: Bolivia. Beni: Espíritu, 19 oct. 1980, *S. G. Beck 5211* (holotipo, LPB!; isotipo, SI!).

Plantas anuales, cespitosas, de 18–45 cm de alto; cañas erectas a geniculadas, delgadas, de 1.2–1.4 mm, comprimidas; entrenudos 1 o 2, los inferiores reducidos, los superiores hasta de 8 cm de largo, pajizos, glabros; nudos glabros, castaños. Vainas predominantemente basales, de 2–8 cm, con pelos de base tuberculada sobre toda la superficie, carenadas, los márgenes membranáceos; lígulas membranáceo-ciliadas, de 0.2–0.3 mm, cuello indistinguible; láminas linear-lanceoladas a lanceoladas, de 5–16 × 0.4–0.7 mm, planas, estriadas, densamente pilosas en ambas caras, con pelos de base tuberculada hasta de 2 mm, base continuándose imperceptiblemente con la vaina, de ápice agudo a subagudo, los márgenes pestañosos. Inflorescencias terminales o axilares, de 4–7 × 0.7–2 cm, exertas o subincluidas en las vainas; 1–3 pedúnculos naciendo en el último nudo caulinar, hasta de 20 cm, filiformes, estriados, glabros; eje principal anguloso, de 1–2.5 cm, 0.3–0.4 mm diám.; 2–4 racimos, ascendentes, divergentes, alternos, los superiores conjugados; raquis de los racimos triquetro, de 2.5–6 cm, glabro, los bordes escabrosos; pedicelos de 0.15–0.3 mm, glabros. Espiguillas anchamente elipsoides, 1.5–1.7 × 0.6–0.8 mm, glabras o con algunos pelos cortos entre los nervios, pajizas, de ápice agudo; gluma superior y lema inferior subiguales; gluma superior de 1.5–1.7 mm, membranácea, 2–4-nervia, el nervio medio ausente; lema inferior glumiforme, 2-nervia, el nervio medio ausente; antecio superior elipsoide, de 1.5–1.6 × 0.6–0.8 mm, pajizo, finamente papiloso, glabro, de ápice obtuso; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, de 0.2–0.3 mm; estambres 3, anteras de 0.6–0.8 mm. Cariopsis elipsoide, de 1.3 × 0.7 mm; hilo oblongo; embrión 1/2 de la cariopsis.

Hábitat y distribución. Esta es una especie endémica de Bolivia, donde crece en los departamentos Beni y Santa Cruz, en campos húmedos y secos entre los 190 y 500 m.s.n.m.

Discusión. *Axonopus boliviensis* pertenece a la serie *Axonopus* por tener raquis glabro a escabroso,

espiguillas con gluma superior y lema inferior con nervio medio ausente a poco desarrollado y por poseer antecio superior pajizo. Esta especie es morfológicamente afín a *A. fissifolius* y a *A. hirsutus* G. A. Black. *Axonopus boliviensis* se distingue de *A. fissifolius* principalmente por poseer, la última especie, vainas y láminas glabras (vs. vainas y láminas pilosas en *A. boliviensis*), láminas de 2–4(–5) mm de ancho (vs. 4–7 mm) y espiguillas más angostas sobre pedicelos angostos. *Axonopus hirsutus* se aparta por ser las plantas perennes con nudos barbados (vs. plantas anuales con nudos glabros a pilosos en *A. boliviensis*).

Material adicional examinado. BOLIVIA. **Beni:** Ballivián, Espíritu, *Beck 5210* (LPB, SI). **Santa Cruz:** Velazco, Estancia Flor de Oro, *Nee 41480* (MO, SI, USZ).

5. Axonopus brasiliensis (Spreng.) Kuhlm., Relat. Comiss. Linhas Telegr. Estratég. Matto Grosso Amazonas 67(11): 47. 1922. Basiónimo: *Eriochloa brasiliensis* Spreng., Syst. Veg. 1: 249. 1824 [1825]. *Paspalum brasiliense* (Spreng.) Hack., Ergebn. Bot. Exp. Sudbras. 1: 7. 1906. TIPO: Brasil. s. loc., s.d., *Otto s.n.* (holotipo, B!; isotipo, US!).

Paspalum dissitiflorum Trin., Gram. Panic. [Trinius] 92. 1826. *Paspalum dissitiflorum* Trin. ex Nees, Fl. Bras. Enum. Pl. 2(1): 32. 1829, nom. illeg. superfl., como "*Paspalus dissitiflorus*". *Axonopus dissitiflorus* (Trin.) Chase, Proc. Biol. Soc. Wash. 24: 135. 1911. *Axonopus dissitiflorus* (Trin.) Kuhlm., Relat. Comiss. Linhas Telegr. Estratég. Matto Grosso Amazonas 67(11): 87. 1922, nom. illeg. superfl. TIPO: Brasil. Barra da Jiquitiba, in campis glareosis, nov. 1824, *G. H. von Langsdorff s.n.* (holotipo, LE-TRIN 0445.01!; isotipos, B!, LE-TRIN 0445.03!, LE foto y fragm. en SI!, LE fragm. en US 2854664!).

Lappagopsis bijuga Steud., Syn. Pl. Glumac. 1: 112. 1854. *Axonopus bijugus* (Steud.) Chase, Proc. Biol. Soc. Wash. 24: 136. 1911. TIPO: Brasil. Santa Catarina: Ilha de Santa Catarina, s.d., *J. S. D. d'Urville s.n.* (lectotipo, designado por Black [1963: 159]; isotipos, BAA!, US!).

Plantas perennes, densamente cespitosas, cortamente rizomatosas, de base compacta con numerosas vainas secas y fibrosas; cañas de 30–95 cm × 0.8–1.8 mm diám., cilíndricas en la base y algo comprimidas hacia la parte superior; entrenudos 1–2(3), de 6–20 cm, pajizos, glabros, castaños; nudos castaños, glabros o pilosos. Vainas predominantemente basales, de 2–9 cm, glabras, aquilladas, estriadas, con los márgenes membranáceos, pestañosos hacia la porción superior; vainas superiores de 10–18 cm; lígulas membranáceo-ciliadas, de 0.2–0.3 mm, cuello indistinguible, glabro; láminas angostamente lineares a filiformes, de 5–35 × 0.1–0.3 cm, firmes, involutas a conduplicadas, algunas veces planas en la región media, glabras a densamente pilosas, de base angosta continuándose imperceptiblemente con la vaina, ápice agudo, los márgenes pestañosos, con pelos tuberculados hasta de 2 mm; láminas superiores reducidas. Inflorescencias terminales, de 60–120 × 1–3 mm, exertas; pedúnculos de 12–42 cm, cilíndricos, con un lado surcado, lisos, pajizos, glabros; eje principal anguloso, de 0–20 × 0.6–0.8 mm, hirsuto, con pelos papilosos; 2–4(–6) racimos, ascendentes, divergentes, alternos, los superiores aproximados; raquis de los racimos triquetro, de 30–120 × 0.4–0.6 mm, con los márgenes largamente pestañosos, con pelos hasta de 4 mm; pulvínulos densamente pilosos; pedicelos triquetros, de 0.3–0.5 mm, pilosos hacia la base, escabriúsculos. Espiguillas largamente ovoides, de 2.1–4.5 × 0.7–1 mm, de ápice agudo, pajizas a púrpuras, pilosas en la base y densamente hirsutas en el dorso, con pelos tuberculados, blanquecinos, hasta de 4 mm dispuestos entre los nervios y el ápice; gluma superior 0.2–0.5 mm mayor que la lema inferior; gluma superior de 2.1–4.5 mm, membranácea, 5-nervia, con los nervios prominentes, los submarginales menos manifiestos; lema inferior glumiforme, 3(–5)-nervia; antecio superior largamente elipsoide, de 2–4 × 0.7–1 mm, 0.2–0.5 mm más corto que la espiguilla, cartilaginoso, castaño oscuro a negruzco; lema finamente papilosa, de ápice agudo, con un mechón de pelos cortos, blanquecinos; pálea de textura y ornamentación similar a la lema, glabra o cortamente pubescente hacia el ápice; lodículas 2, de 0.2–0.3 mm, membranáceas, cuneadas; estambres 3, anteras de 1.8–2 mm, purpúreas. Cariopsis no vista.

Hábitat y distribución. *Axonopus brasiliensis* es una especie sudamericana: en Brasil crece en el centro y este hasta los estados de Paraná, Rio Grande do Sul y Santa Catarina; en Paraguay se halla en Amambay y Concepción; y en Bolivia se encuentra en Beni y Santa Cruz. Habita en campos abiertos, entre los 100 y 1500 m.s.n.m., en suelos arenosos, flojos, bien drenados; es frecuente en campos sujetos a fuegos períodicos, por lo que es común observar, en los ejemplares de herbario, restos de vainas fibrosas y quemadas en la base de las plantas.

Nombres vulgares. "Capim-branco", "Colônia" (Smith et al., 1982: 1138), "Kapi'cerro ari" (Morrone et al., 1994: 32).

Discusión. *Axonopus brasiliensis* pertenece a la sección *Lappagopsis* (Steud.) Chase por poseer raquis de la inflorescencia híspido, con pelos blanquecinos, gluma superior y lema inferior papiloso-pilosas y antecio superior castaño oscuro. La especie es

morfológicamente afín a *A. herzogii* (Hack.) Hitchc. (véase observaciones bajo esta última especie).

Paspalum tenuis, publicado por Trinius (1826: 26), y *P. tener*, publicado por Nees (1829: 32), son pro sinónimos de *Axonopus brasiliensis* y ambos son nomina nuda.

Material adicional examinado. BOLIVIA. **Beni:** Prov. Ballivián, 157 km de El Mirador hacia Riberalta, 4 km después del desvío a Cobija, *Michel & Beck 2059* (K, LPB, SI). **Santa Cruz:** Prov. Chiquitos, Serranía de Santiago, 3 km N of Santiago de Chiquitos, *Killeen 2788* (F, LPB, MO, USZ). BRASIL. **Paraná:** Jaguariaiva, Parque Estadual do Cerrado, jonto ao Canyon, *Longhi-Wagner et al. 9461a* (F, SI). **Rio Grande do Sul:** Torres, Praia Real, *Longhi-Wagner & Hefler 9087* (F). **Santa Catarina:** Campo Alegre, Morro Iquererim, *Smith & Klein 7405* (US). PARAGUAY. **Amambay:** Parque Nacional Cerro Corá, Remonta Cué, *Morrone & Pensiero 548* (MO, SI). **Concepción:** Zwischen Rio Apa und Rio Aquidabán, 1908/1909, *Fiebrig 4694* (F, G).

6. Axonopus capillaris (Lam.) Chase, Proc. Biol. Soc. Wash. 24: 133. 1911. Basiónimo: *Paspalum capillare* Lam., Tabl. Encycl. 1: 176. 1791. TIPO: Guayana Francesa. Cayenne, s.d., *J. B. Leblond s.n.* (holotipo, P-LA!; isotipo, P fragm. en US 2942169!).

Paspalum extenuatum Nees, Fl. Bras. Enum. Pl. 2(1): 25. 1829, como "*Paspalus extenuatus*". *Axonopus extenuatus* (Nees) Kuhlm., Relat. Comiss. Linhas Telegr. Estratég. Matto Grosso Amazonas 67(11): 87. 1922. TIPO: Brasil. Bahia: Joazeiro et Terram Novam, s.d., *K. F. P. von Martius s.n.* (holotipo, M no visto; isotipos, LE TRIN 453.01!, LE foto y fragm. en SI!, M fragm. en US 2854674!).

Paspalum minutum Trin., Linnaea 10(3): 293. 1836. TIPO: Perú. Cuchero, 1829, *E. F. Poeppig s.n.* (holotipo, LE TRIN 494.01!, LE foto en SI!; isotipos, LE fragm. en SI!, LE fragm. en US 2942168!).

Plantas anuales, pequeñas, delicadas, formando matas circulares, cespitosas; cañas geniculadas de 7–60 cm × 0.5–2 mm diám., comprimidas; entrenudos 2–5, de 1–30 cm, levemente estriados, surcados, pajizos, glabros; nudos glabros a pubérulos, castaños. Vainas predominantemente basales, de 2–10 cm, usualmente más cortas que los entrenudos, aquilladas, glabras, con los márgenes membranáceos, pestañosos hacia la porción superior; vainas superiores hasta de 14 cm, distantes entre sí; lígulas membranáceo-ciliadas, de 0.3–0.5 mm, con pelos cortos, blanquecinos; cuello ligeramente distinguible, glabro; láminas lanceoladas, de (3–)4–12(–20) × 0.4–0.8(–1) cm, planas, glabras a híspidulas, con pelos tuberculados, blanquecinos, base subcordada, ápice agudo a acuminado, los márgenes membranáceos, escabriúsculos, glabros o pestañosos hacia la porción basal. Inflorescencias terminales y axilares de 1.4–5 × 1–2 cm, exertas o subincluidas en las vainas foliares; pedúnculos 1–4 naciendo del último nudo caulinar, de 6–24 cm, filiformes, surcados, glabros; eje principal anguloso, de 0–25 × ca. 0.3 mm, con 2–6 racimos, ascendentes, divergentes, los superiores aproximados a conjugados; raquis de los racimos triquetro, de 20–40(–60) × 0.3–0.5 cm, glabro, con los márgenes escabrosos; pulvínulos cortamente pilosos; pedicelos de 0.15–0.25 mm, escabriúsculos, glabros. Espiguillas anchamente elipsoides, de 0.9–1.3(–1.5) × 0.5–0.7 mm, de ápice agudo a subagudo, pajizas, glabrescentes a pubescentes, con pelos delicados, adpresos, blanquecinos, formando hileras longitudinales entre los nervios; gluma superior y lema inferior subiguales, tan largas como el antecio superior; gluma superior de 0.9–1.3(–1.5) mm, membranácea-hialina, 2–4-nervia, con nervios poco manifiestos, nervio medio ausente; lema inferior glumiforme, 2–4-nervia; antecio superior elipsoide, de 0.8–1.2(–1.4) × 0.5–0.6 mm, pajizo a castaño a la madurez, obtuso, finamente papiloso, glabro; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, ca. 0.15 mm, membranáceas, cuneadas; estambres 3, anteras de 0.3–0.5 mm. Cariopsis oblongoide, de 1 × ca. 0.5 mm; hilo anchamente elíptico; embrión 1/3–1/2 del tamaño de la cariopsis.

Hábitat y distribución. *Axonopus capillaris* es una especie de amplia distribución: habita desde América Central, norte de Sudamérica (Judziewicz, 1990: 91; Pohl & Davidse, 1994: 358) hasta el sur de Brasil (Paraná) y Bolivia (La Paz, Cochabamba, Santa Cruz). Crece en campos, en suelos arenosos, desde el nivel del mar hasta los 1100 m.s.n.m. Black (1963), Judziewicz (1990) y Valls et al. (2001) señalan que *A. capillaris* habita en Paraguay sin indicar ejemplar de referencia. Hasta el presente no se ha localizado ningún ejemplar de esta especie para Paraguay por lo que su presencia se considera dudosa.

Número cromosómico. Se ha completado, para *Axonopus capillaris* un recuento cromosómico de $n = 20$ (Pohl & Davidse, 1971: 299 sub *A. capillaris* (Lam.) Chase).

Discusión. *Axonopus capillaris* pertenece a la serie *Capillares* G. A. Black y se distingue por incluir plantas anuales, cespitosas, formando matas circulares, gráciles, de 7–60 cm de alto, con láminas lanceoladas, planas, de base subcordada, distribuidas laxamente a lo largo de las cañas, inflorescencias con panojas que no superan los 5 cm de largo, con pocos (2–4[–6]) racimos, espiguillas de 0.9–1.3(–1.5) mm de longitud y antecio superior del mismo tamaño que la espiguilla, de ápice glabro y de

color castaño a la madurez. Esta especie es afín a *A. fissifolius* pero la última se distingue por ser plantas perennes, usualmente estoloníferas, con láminas lineares, de base angostada, espiguillas elipsoides de 1.6–2 mm de largo por 0.5–0.6 mm de ancho y antecio superior pajizo.

Black (1963), Judziewicz (1990) y Valls et al. (2001) señalan que *Axonopus capillaris* habita en Paraguay sin indicar ejemplar de referencia. Hasta el presente no se ha localizado ningún ejemplar de esta especie para Paraguay por lo que su presencia se considera dudosa.

Material adicional examinado. BOLIVIA. **Cochabamba:** Cochabamba, *Bang 872* (MO). **La Paz:** Prov. Nor Yungas, arriba de Coroico, *Beck 17548* (MO). **Santa Cruz:** Parque Nac. Noel Kempff, Campamento los Fierros–Aserradero El Tarbo, *Mostacedo et al. 1563a* (MO, SI). BRASIL. **Paraná:** 3 km NE of São João da Aliança, *Anderson 7749* (F, MO).

7. Axonopus caulescens (Mez) Henrard, Blumea 4(3): 510. 1941. Basiónimo: *Paspalum caulescens* Mez, Bot. Jahrb. Syst. 56(125): 10. 1921. TIPO: Guyana. Mazaruni–Potaro: Amazonas Expedition, "am Ufer eines Baches beim Dorfe Roraima", 1200 m, dic. 1903, *E. Ule 8533* (holotipo, B!; isotipos, IAN no visto, K no visto, L 600190!, MG no visto, U!, US 2942172! [fragm. ex B], US 91016! [fragm. ex K]). Figura 2.

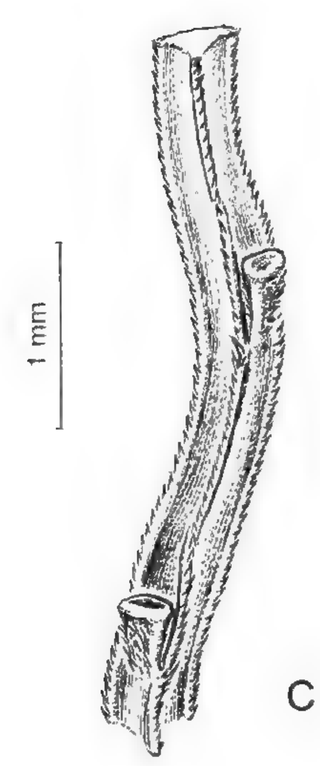
Plantas perennes, cespitosas, estoloníferas, cortamente rizomatosas; cañas de 30–50(–60) × 0.2–0.4 cm diám., erectas a geniculadas, teretes hacia la base y luego comprimidas hacia la porción superior, simples a conspicuamente ramificadas en la porción media; entrenudos numerosos, de 1–5 cm, los inferiores aproximados, los superiores distanciados; nudos castaños, glabros a densamente pilosos. Vainas distribuidas más densamente hacia la porción superior, superpuestas, de 1–4 cm, glabras, los márgenes membranáceos, glabros a pestañosos hacia la porción superior; lígulas membranáceo-ciliadas, de 0.4–0.7 mm; cuello distinguible, glabro a piloso; láminas linear-lanceoladas, de 2–6(–8) × 0.2–0.3 cm, falcadas, densamente distribuidas hacia la porción superior de las cañas, planas o más comúnmente plegadas, glabras a pilosas en ambas caras, de ápice agudo a subagudo, los márgenes escabriúsculos, glabros a densamente pestañosos hacia la región basal. Inflorescencias terminales y axilares de 3–6 × 1.5–3 cm, exertas; 1–3 pedúnculos naciendo del último nudo caulinar, de 6–25 cm × 0.3–0.4 mm, filiformes, finamente estriados, glabros; eje principal anguloso, de 0–1.5 × 0.4–0.5 mm, escabriúsculo; racimos 2–4, ascendentes, divergentes, alternos a conjugados; raquis de los racimos triquetro, de 20–70 × 0.2–0.4 mm, con los márgenes escabriúsculos; pulvínulos pilosos; pedicelos triquetros, de 0.3–0.7 mm, glabros o finamente pubescentes. Espiguillas largamente elipsoides, de 2.3–2.8 × 0.5–0.8 mm, de ápice agudo a subagudo, pajizas a castañas, pilosas, con pelos distribuidos en la base y longitudinalmente a lo largo de los espacios internervales, blanquecinos, dorados o con tíntes purpúreos; gluma superior y lema inferior subiguales, 0.2–0.4 mm más largas que el antecio superior; gluma superior 2.3–2.8 mm, membranácea, 5(–7)-nervia; lema inferior glumiforme, 5-nervia; antecio superior largamente elipsoide, 2.1–2.6 × 0.5–0.7 mm, de ápice agudo, pajizo, finamente papiloso, con un mechón de pelos blanquecinos en el ápice, hasta de 0.5 mm; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, 0.2–0.3 mm, cuneadas; estambres 3, anteras de 1.4–1.6 mm, purpúreas. Cariopsis no vista.

Hábitat y distribución. *Axonopus caulescens* es una especie que crece en el norte de Sudamérica, en Venezuela, Guyana (Judziewicz, 1990: 93), norte de Brasil (Black, 1963: 106) y se cita por primera vez para Bolivia (La Paz). Es una especie común en suelos rocosos, arenoso-pedregosos, y en sabanas, formando matas definidas, entre los 1660 y 2300 m.s.n.m.

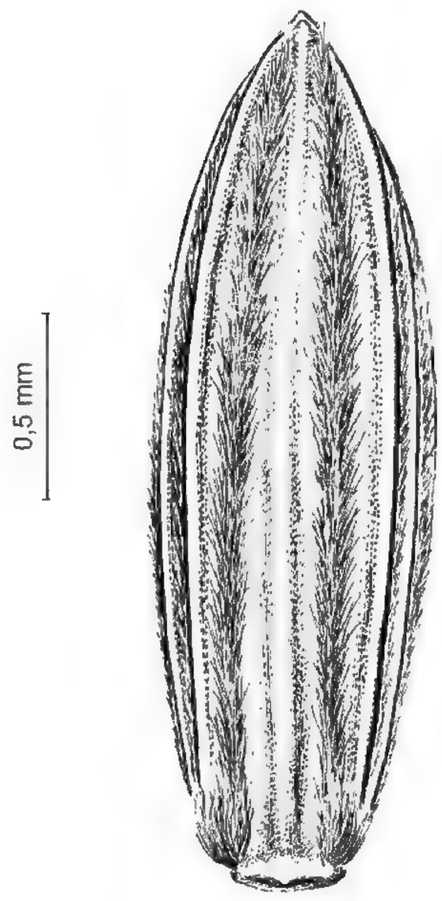
Discusión. *Axonopus caulescens*, miembro de la serie *Barbigeri*, se caracteriza principalmente por sus cañas plurinodes de entrenudos cortos, ramificadas en la porción media, con vainas notoriamente dísticas, superpuestas a lo largo de la caña y láminas falcadas, con apariencia fastigiada.

Black (1963) ubica a *Axonopus caulescens* dentro de la subserie *Scopari* G. A. Black, la cual se caracteriza porque sus especies poseen láminas anchas, nunca involutas o filiformes, de ápice acuminado o agudo y con el nervio medio presente, conspicuo o ausente. Sin embargo, las láminas de *A. caulescens* son angostas, hasta de 3 mm de ancho, por lo que su inclusión en la subserie *Scopari* es dudosa.

La presencia de un hábito notoriamente ramificado en *Axonopus caulescens* la relaciona superficialmente con *A. ramosus* Swallen, especie perteneciente a la serie *Suffulti* y que habita en Surinam, Guayana Francesa y norte de Brasil. Esta última especie se distingue por tener antecio superior castaño (vs. pajizo en *A. caulescens*), espiguillas de menor tamaño, de 1.2–1.6 mm de largo (vs. 2.3–2.8 mm) y gluma superior y lema inferior 2–3(4)-nervias (vs. 5[–7]-nervias).



C



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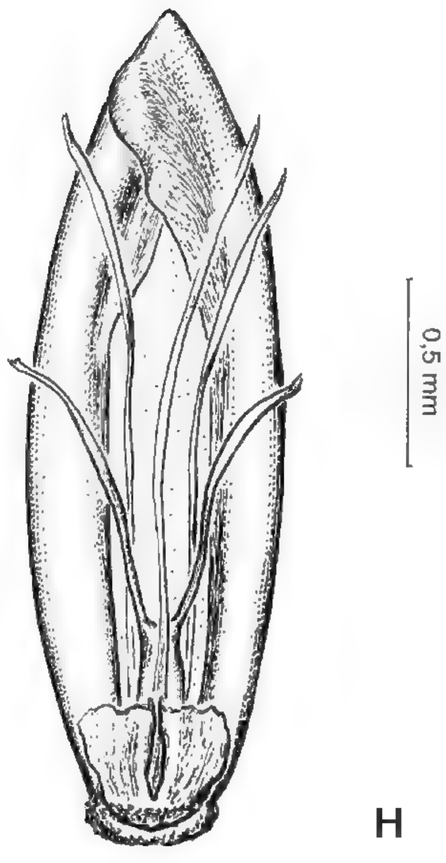

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Figura 2. *Axonopus caulescens* (Mez) Henrard. —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Espiguilla, vista del lado de la gluma superior. —E. Espiguilla, vista del lado de la lema inferior. —F. Antecio superior, vista dorsal mostrando la lema superior. —G. Antecio superior, vista ventral mostrando la pálea superior. —H. Pálea superior, lodículas y filamentos estaminales (*Miranda et al. 833*, LPB).

Material adicional examinado. BOLIVIA. **La Paz:** Murillo, valle del Río Zongo, *Solomon 18850* (LPB, MO, SI); Franz Tamayo, senda Apolo–San José de Uchupiamonas, camino a Río Piñalito, *Miranda et al. 858* (LPB, MO, SI). VENEZUELA. **Bolívar:** Distr. Piar, Cerro Kurún-tepui, *Huber et al. 8188* (MO).

8. Axonopus chrysoblepharis (Lag.) Chase, Proc. Biol. Soc. Wash. 24: 134. 1911. Basiónimo: *Cabrera chrysoblepharis* Lag., Gen. Sp. Pl. [Lagasca]: 5. 1816. *Paspalum chrysoblephare* (Lag.) Döll, Fl. Bras. 2(2): 119. 1877. TIPO: Panamá. s. loc., s.d., *L. Née s.n.* (holotipo, MA no visto; isotipo, MA fragm. en BAA!).

Paspalum excavatum Nees ex Trin., Gram. Panic. [Trinius]: 88. 1826. *Axonopus excavatus* (Nees ex Trin.) Henrard, Blumea 4(3): 509. 1941. TIPO: Brasil. Minas Gerais: s. loc., s.d., *K. F. P. von Martius s.n.* (holotipo, M no visto; isotipos, BM!, M fragm. en US 2942571!, M fragm. en SI!).

Plantas de duración indefinida, cespitosas; cañas erectas a decumbentes, de 20–100 cm × 1–3 mm diám., simples o ramificadas en la base, cilíndricas a comprimidas; entrenudos 4–10, de 3–10 cm, pajizos a castaños, glabros; nudos castaños, glabros a pilosos, con pelos hasta de 2 mm, dorados. Vainas de 4–11 cm, glabras a esparcidamente hirsutas, con pelos hasta de 1 mm, los márgenes membranáceos, glabros o con un margen pestañoso, más densamente hacia la porción distal; vainas superiores hasta de 15 cm; lígulas membranáceo-ciliadas, de 0.5–1.1 mm; cuello distinguible, glabro a piloso; láminas linear-lanceoladas, de 5–20 × 0.5–1 mm, planas a conduplicadas, glabras a pilosas en ambas caras, más densamente en la cara adaxial hacia la porción basal, con pelos papilosos, base redondeada y ápice agudo a cortamente acuminado, los márgenes escabriusculos, pestañosos, con pelos tuberculados hasta de 2 mm, dorados, más frecuentemente hacia la porción basal. Inflorescencias terminales o axilares, de 5–16 × 3–5 cm; pedúnculos 1–4, de 10–35 cm, cilíndricos, surcados, lisos, glabros o pubérulos hacia la región apical; eje principal anguloso, de 0–15 × 0.7–0.9 mm, glabro; racimos 3–8(–10), ascendentes, divergentes, subdigitados, rígidos, falcados; raquis de los racimos triquetro, de 4–10 × 0.1–0.15 cm, terminando en una prolongación estéril, los márgenes largamente pestañosos, con pelos hasta de 3 mm, tuberculados, dorados; pulvínulos pilosos; pedicelos reducidos o nulos; espiguillas inmersas en cavidades del raquis, cupuliformes, los márgenes de la cúpula con pelos tuberculados, dorados. Espiguillas elipsoides a ovoides, de 0.9–1.6 × 0.5–0.7 mm, glabras, de ápice subagudo a obtuso, violáceas a doradas; gluma superior y lema inferior subiguales, tan largas como el antecio superior; gluma superior 0.9–1.6 mm, hialina, delicada, 2-nervia, el nervio medio ausente; lema inferior glumiforme, 2-nervia; antecio superior ovoide, de 0.9–1.6 × 0.5–0.6 mm, castaño oscuro, levemente pajizo en el ápice y en la base, finamente papiloso, el ápice subagudo a obtuso, glabro; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, ca. 0.1 mm; estambres 3, anteras de 0.9–1.1 mm, purpúreas. Cariopsis ovoide, ca. 1 mm.

Hábitat y distribución. *Axonopus chrysoblepharis* es una especie de amplia distribución: habita desde Guatemala (Pohl & Davidse, 1994: 359) hasta Bolivia (Santa Cruz, Beni, La Paz), norte, centro y sudeste de Brasil (Paraná) y Paraguay (Amambay, Concepción). Este taxón crece en suelos arenosos y arcillosos de áreas húmedas o secas, entre los 100 y 1500 m.s.n.m.

Nombre vulgar. "Kapi' i cerro ári" (Paraguay, Morrone et al., 1994: 34).

Número cromosómico. *Axonopus chrysoblepharis* es una especie diploide, habiéndose citado recuentos cromosómicos de $n = 10$ (Davidse & Pohl, 1974: 319 sub *A. chrysoblepharis* (Lag.) Chase); $2n = 20$ (Norrmann et al., 1994: 769 sub *A. chrysoblepharis* (Lag.) Chase); $2n = 20 + 2B$ (Pohl & Davidse, 1971: 299 sub *A. chrysoblepharis*); $2n = 20 + 4B$ (Pohl & Davidse, 1994: 359 sub *A. chrysoblepharis*).

Discusión. *Axonopus chrysoblepharis* es un miembro de la sección *Cabrera* por tener raquis conspicuamente pestañoso, con pelos de base tuberculada, dorados, y terminando en una prolongación estéril, gluma superior y lema inferior glabras a esparcidamente pilosas y antecio superior castaño oscuro a la madurez. La especie está morfológicamente relacionada con *A. aureus*, de la que es fácilmente distinguible por la disposición de las espiguillas en el raquis, las que se hallan inmersas en cavidades o excavaciones (vs. espiguillas no en cavidades o excavaciones en *A. aureus*).

Giraldo-Cañas (2001) señala que la lema inferior es 2- o 3-nervia, con los nervios marcados. Sin embargo esta característica no se observó en los ejemplares analizados, siendo la lema inferior 2-nervia.

Renvoize (1998) considera a *Axonopus excavatus* como un taxón independiente de *A. chrysoblepharis*, y la distingue principalmente por su hábito anual. Sin embargo, de acuerdo con Black (1963), Garófalo-Spalding (1990) y Giraldo-Cañas (2001), el hábito anual o perenne depende de las condiciones ambientales en que se desarrolla la especie y por lo tanto, la longevidad de la especie sería una respuesta

ecológica que no puede ser usada como característica diagnóstica para separar ambos taxones. Consecuentemente, se considera a *A. excavatus* bajo la sinonimia de *A. chrysoblepharis*.

Material adicional examinado. BOLIVIA. **Beni:** Ballivián, Ea. Biológica del Beni, 40 km al E de San Borja, *Killeen 2818* (LPB, MO, USZ). **La Paz:** Nor Yungas, Coripata, 10 km hacia Arapata, *Beck 21085* (K, LPB, SI). **Santa Cruz:** Ñuflo de Chávez, Ea. Las Madres, 15 km N of Concepción, *Killeen 894* (F, LPB, MO, USZ). BRASIL. **Paraná:** Capão Bonito, *Dusén 16838* (F, MO, SI, US). PARAGUAY. **Amambay:** Sierra de Amambay, *Hassler & Rojas 10747* (BAA, G, US). **Concepción:** Zwischen Río Apa und Río Aquidabán, *Fiebrig 5048* (BAA, F, G).

9. Axonopus comans (Trin. ex Döll) Kuhlm., Relat. Comiss. Linhas Telegr., Estratég. Matto Grosso Amazonas 67(11): 87. Marzo 1922. Basiónimo: *Paspalum comans* Trin. ex Döll, Fl. Bras. [Martius] 2(2): 109. 1877. *Axonopus comans* (Trin. ex Döll) Henrard, Meded. Rijks-Herb. 47: 2. [dic. 1922], nom. illeg. superfl. TIPO: Brasil. São Paulo: Ribeirão d'Arca, 1818, *F. Sellow s.n.* (holotipo, B!; isotipos, B fragm. en US 2942141!, LE TRIN 0427.01!, LE foto en SI!).

Plantas perennes, cespitosas, cortamente rizomatosas; cañas simples, erectas, de 45–70 cm de alto, paucinodes, comprimidas o no; entrenudos 1–3, de 8–22 cm, lisos, pajizos, glabros; nudos glabros a esparcidamente pilosos, pajizos a castaños. Vainas predominantemente basales, de 5–12 cm, aquilladas, glabras a esparcidamente pilosas, con los márgenes membranáceos, pestañosos hacia la porción superior; lígulas membranáceo-ciliadas, de 0.2–0.3 mm; cuello indistinguible, glabro; láminas filiformes, de (8–)30–48 cm × 0.3–1.2 mm, rígidas, glabras, de base más angosta que las vainas, el ápice agudo, pungente, márgenes membranáceos, pestañosos hacia la porción basal. Inflorescencias terminales de 6–12 × 2–5 cm, exertas; pedúnculos de 15–50 cm, cilíndricos, glabros, finamente estriados; eje principal anguloso, hasta de 4 cm, 0.5–0.8 mm de ancho, surcado, glabro; racimos 2–4(5), ascendentes, alternos, los superiores aproximados a conjugados; raquis de los racimos triquetro, de 40–90 × 0.3–0.6 mm, glabro, con los márgenes finamente escabriúsculos; pulvinulos glabros; pedicelos triquetros, de 0.3–0.6 mm, escabriúsculos. Espiguillas elipsoides, de (3.6–)4–5 × 0.8–1.2 mm, de ápice acuminado, pajizas a verdosas, glabras a esparcidamente pilosas, con pelos suaves, adpresos; gluma inferior y lema superior subiguales, tan largas como el antecio superior o superándolo hasta 0.3 mm; gluma superior de (3.6–)4–5 mm, membranácea, 5–7-nervia, con los nervios prominentes; lema inferior glumiforme, 5–7-nervia; antecio superior elipsoide, de 3.3–4.7 × 0.8–1.1 mm, pajizo, endurecido, finamente papiloso, de ápice agudo a subgudo, con un mechón de pelos blanquecinos hacia la porción distal; pálea de similar textura y ornamentación que la lema, glabra o esparcidamente pilosa sobre los márgenes superiores; lodículas 2, de 0.2–0.3 mm, cuneadas; estambres 3, anteras de 2.4–2.7 mm, purpúreas. Cariopsis no vista.

Hábitat y distribución. *Axonopus comans* habita en el centro y sudeste de Brasil, en el estado de Paraná, y en Paraguay oriental, en los departamentos Amambay y Guairá. Esta especie se halla en campos abiertos, en borde de arroyos y de bosques; es frecuente en áreas sujetas a fuegos periódicos, siendo común hallar en las bases de las plantas restos de vainas quemadas.

Nombres vulgares. "Kapi'i cerro", "Kapi'i estero" (Paraguay, Morrone et al., 1994: 37).

Discusión. *Axonopus comans*, miembro de la serie *Barbigeri*, es morfológicamente afín a *A. uninodis* (Hack.) G. A. Black (véanse diferencias morfológicas bajo *A. uninodis*).

Material adicional examinado. BRASIL. **Paraná:** Camino de Castro a Tibaji, *Morrone & Zuloaga 5375* (SI); Ponta Grossa, *Dusén 2523* (MO); Mun. Tijucas do Sul, Rincão, *Hatschbach 40445* (MBM, MO). PARAGUAY. **Amambay:** In regione calcar. Cursus sup. Fl. Apa, *Hassler 11942* (BAA, G). **Guairá:** Cordillera de Villarica, *Balansa 104* (BAA, G).

10. Axonopus compressus (Sw.) P. Beauv., Ess. Agrostogr. 12, 154. 1812. Basiónimo: *Milium compressum* Sw., Prodr. [Swartz] 24. 1788. TIPO: Jamaica. s. loc., s.d., *Shakespear s.n.* (holotipo, S!; isotipo, BM 576790 no visto, BM foto en SI!).

Axonopus compressus var. *australis* G. A. Black, Advancing Frontiers Pl. Sci. 5: 81. 1963. TIPO: Argentina. Misiones: Posadas, La Granja, 11 nov. 1907, *E. L. Ekman 599* (holotipo, US 602533!, US foto en SI!; isotipo, US fragm. en SI!).

Axonopus compressus var. *macropodius* (Steud.) G. A. Black, Advancing Frontiers Pl. Sci. 5: 82. 1963. Basiónimo: *Paspalum macropodium* Steud., Syn. Pl. Glumac. 1: 19. 1853. TIPO: Ecuador. Guayas: banks of Guayaquil River, s.d., *W. Jameson 556* (holotipo, P!; isotipos, K no visto, P fragm. en SI!, US 80084!, US fragm. en SI!).

Plantas perennes, cespitosas a fuertemente estoloníferas o rizomatosas; cañas erectas a decumbentes, de 10–70(–80) cm de alto; entrenudos 1–4, los inferiores cortos, los superiores hasta de 15 cm;

nudos glabros a pilosos, castaños. Vainas de 3–11 cm, las inferiores más largas que los entrenudos, glabras, los márgenes membranáceos, glabros a pestañosos; lígulas membranáceo-ciliadas, de 0.3–0.7 mm; cuello distinguible, glabro; láminas linear-lanceoladas a lanceoladas, de 3.5–14(–25) × (0.5–) 0.7–1.2 cm, con prefoliación convoluta, glabras a esparcidamente pilosas en ambas caras, de base subcordada y ápice obtuso a subagudo, los márgenes escabriúsculos, glabros a pestañosos hacia la base, con pelos tuberculados. Inflorescencias terminales y axilares, de 4–12 × 2–5 cm, exertas; 1–4 pedúnculos naciendo del último nudo caulinar, hasta de 35 cm, exertos a subincluidos en las vainas foliares, teretes, glabros, lisos; eje principal de 0–2.5 cm, anguloso, glabro, liso; racimos (2)3–6(–9), ascendentes, divergentes, alternos, los superiores conjugados; raquis de los racimos triquetro, de 30–90(–130) × ca. 0.4–0.7 mm, glabro; pulvínulos glabros; pedicelos 0.2–0.4 mm, tan anchos como la base de la espiguilla, escabriúsculos. Espiguillas ovoides, de (1.8–)2–2.6(–3) × 0.8–1.2 mm, de ápice acuminado, glabras a esparcidamente pilosas, con pelos adpresos a lo largo de los nervios marginales y el ápice; gluma superior y lema inferior subiguales, 0.4–0.8 mm más largas que el antecio superior; gluma superior de 2–2.6(–3) mm, 2–4(5)-nervia, con el nervio medio generalmente ausente; lema inferior glumiforme, 2–4(5)-nervia, nervio medio generalmente ausente; antecio superior elipsoide, de 1.4–2.4 × 0.7–0.9 mm, de ápice obtuso, pajizo, finamente papiloso, piloso junto al ápice, con un mechón de pelos blanquecinos; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, de 0.2–0.3 mm; anteras 3, estambres de 1.2–1.5 mm. Cariopsis elipsoide, de 1.6 × 0.6 mm; hilo oblongo, subbasal; embrión 1/3 del largo de la cariopsis.

Hábitat y distribución. *Axonopus compressus* es una especie originaria de los trópicos de América, introducida en el Viejo Mundo en África, en Camerún, Ghana, Islas Seychelles, Liberia, Madagascar, Mauricio, República Democrática del Congo, Sierra Leona, Tanzania y Zambia (Black, 1963: 79); en Asia se halla en Australia, Borneo, Fiji, Filipinas, India, Japón y Sumatra (Black, 1963: 80). Esta especie es frecuente en campos y sabanas húmedas, bordes de caminos, claros de bosque y lomas arenosas. Muy utilizada como césped ("carpet grass") y como forraje.

Nombres vulgares. "Kapi'ipe", "kapi'ipe kavaju", "pasto jesuita" (Paraguay, Morrone et al., 1994: 38); "capim cabiú", "capim-de-nó", "grama", "grama-comun-estreita", "grama-de-jardim", "grama-jesuítica", "grama-ouro", "grama-preta", "sempre verde", "sempre-verde-de-folhas-estreitas", "grama-comun", "grama-de-tapete-de-folha-larga", "grama de capao" (Brasil, Smith et al., 1982: 1109); "pasto chato", "pasto jesuita" (Argentina, Morrone et al., 1995a: 13); "pasto chato", "pasto alfombra" (Uruguay, Rosengurtt et al., 1970: 296).

Números cromosómicos. *Axonopus compressus* posee una marcada variabilidad en los niveles de ploídia, los que varían entre un *n* de 10 a 50 (2*x*–10*x*). En esta especie se han citado todos los niveles de ploidía conocidos hasta el presente para el género, incluyendo: *n* = 20 (Pohl & Davidse, 1971: 299 sub *A. compressus* (Sw.) P. Beauv.; Hickenbick et al., 1975: 188 sub *A. jesuiticus* (A. A. Araújo) Valls); *n* = 30 (Hickenbick et al., 1975: 188 sub *A. compressus*); 2*n* = 40 (Pohl & Davidse, 1971: 299 sub *A. compressus*); 2*n* = 56, 60 (Saura, 1948: 54 sub *A. compressus*; Núñez, 1952: 239 sub *A. compressus*).

Discusión. *Axonopus compressus* es miembro de la serie *Axonopus* por poseer antecios claros, pajizos, gluma superior con nervio medio usualmente faltante y ápice de las láminas obtuso a agudo, no setáceo. Esta especie es morfológicamente afín a *A. fissifolius*, distinguiéndose de esta última *A. compressus* principalmente por presentar láminas linear-lanceoladas a lanceoladas (vs. lineares), con prefoliación conduplicada (vs. convoluta), más anchas ([0.5]0.7–1.2 cm vs. 0.2–0.4[0.5] cm de ancho), usualmente con un mayor número de racimos ([dos]tres a seis [a nueve] vs. dos o tres [a seis]), espiguillas de mayor longitud ([1.8]2–2.6[3] mm vs. 1.5–1.8[–2] mm de largo) y antecio superior 0.4–0.6 mm más corto que la espiguilla (vs. del mismo largo o ligeramente menor).

Axonopus compressus presenta una amplia distribución geográfica y una marcada variación en sus caracteres morfológicos vegetativos y reproductivos. Desde el punto de vista morfológico posee una gran variabilidad respecto a la pilosidad de las inflorescencias, el tamaño de los racimos, pedicelos y espiguillas, asi como en la nerviación de la gluma superior y lema inferior y en el color de las anteras. Dentro de este complejo, particularmente en Sudamérica, se han propuesto variedades y especies sobre la combinación de caracteres morfológicos contínuos, marcadamente variables. Hasta tanto no se realice un estudio biosistemático de este complejo, en el presente tratamiento se considera la especie en un sentido amplio.

Material adicional examinado. ARGENTINA. **Buenos Aires:** Ramallo, Isla Las Hermanas, *Burkart 12831* (SI). **Chaco:** Dpto. 1° de Mayo, Colonia Benítez, *Schulz 17328* (SI). **Corrientes:** Dpto. Santo Tomé, *Quarín et al. 2489* (CTES, SI).

Entre Ríos: Delta del Paraná, Arroyo Negro, *Burkart 7593* (SI). **Jujuy:** Dpto. Dr. Manuel Belgrano, Camino de Lagunas de Yala a Reyes, *Zuloaga et al. 6158* (MO, SI). **Misiones:** Dpto. Guaraní, ruta prov. 2, Reserva Ecol. Prov., *Morrone et al. 720* (CTES, MO, SI). **Santa Fe:** Dpto. Gral. Obligado, *Pensiero & Vegetti 2564* (MO, SI). **Tucumán:** Dpto. Chicligasta, Puesto Las Pavas a Saladillo, *Meyer 18019* (CTES). BOLIVIA. **Beni:** Ballivián, Espiritú, en la zona de influencia del Río Yacuma, *Beck 3493a* (LPB). **Chuquisaca:** Entre camp. Rinconada del Bufete y la cumbre de Cerro Bufete, *Holst et al. 4669* (CTES). **La Paz:** Prov. Alto Beni, Popoy antes de llegar a Concepción de la Coop. San José, *Seidel & Vargas 2364* (LPB, MO, SI, USZ). **Pando:** Prov. Nicolás Suárez, Cobija, *Beck 17110* (LPB, SI). **Santa Cruz:** Ñúflo de Chávez, Ea. Las Madres, 9 km N of Concepción, *Killeen 1751* (CTES, F, LPB, MO, SI). **Tarija:** Prov. O'Connor, Entre Ríos, *Caro-Rojas 1553* (LPB). BRASIL. **Paraná:** Porto amazonas, 5 km N, *Hatschbach 3564* (CTES, MBM, MO). **Rio Grande do Sul:** Pôrto Alegre, Morro da Gloria, *Rambo 29048* (LIL, MO). **Santa Catarina:** Camino de Curitiba a Lebón Regis, a 39 km de Curitibanos, *Rúgolo et al. 1587* (MO, SI). PARAGUAY. **Caaguazú:** Arroyo Guaranungua, 28 km S de Arroyo Yhú, *Zardini & Velázquez 24676* (MO, SI). **Caazapá:** Abaí, *Rojas 5804* (BAA). **Canindeyú:** Lagunita, *Jiménez & Marin 1978BJ* (SI). **Central:** vivero Caacupé, *Rojas 12716* (LIL, MO). **Cordillera:** In campis dumetis San Bernardino, *Hassler 2070* (G). **Guairá:** Villarica, *Jörgensen 3538* (BAA, F, LIL, MO). **Itapúa:** Hohenau, *Fiebrig 5581* (BAA). **Misiones:** Ea. La Soledad, *Pedersen 4291* (BAA, CTES). **Paraguarí:** Ayo. Iaguary, Caapucú, *Rosengurtt 5366* (CTES, SI). **San Pedro:** Ruta 3 pasando el Río Aguara Guazú, *Nicora et al. 9872* (SI). URUGUAY. **Canelones:** Parque Nac. del Carrasco, *Rosengurtt 1210* (SI). **Montevideo:** Cerro, *Herter 332* (F, SI). **San José:** Arazatí, *Rosengurtt B795* (BAA).

11. Axonopus cuatrecasasii G. A. Black, Advancing Frontiers Pl. Sci. 5: 147. 1963. TIPO: Colombia. Arauca: Los Llanos, Río Casanare, Esmeralda, 130 m, 19–20 oct. 1938, *J. Cuatrecasas 3882* (holotipo, US 1797918!, US foto en SI!; isotipo, F 1245330!, F foto en SI!).

Plantas perennes, cespitosas, estoloníferas, con estolones delgados; cañas erectas o geniculadas, de 40–120 cm de alto, 1.5–2.2 mm diám., simples o en ocasiones ramificadas en los nudos basales, comprimidas a cilíndricas; entrenudos 3–4, de 2–14 cm, con un lado surcado, verdosos a pajizos, glabros o esparcidamente vilosos; nudos densamente vilosos en toda la superficie o solo en la base, castaños. Vainas de 2–14 cm, menores o iguales que los entrenudos, glabras a densamente vilosas en su cara externa, aquilladas, los márgenes generalmente pestañosos; lígulas membranáceo-ciliadas, de 0.2–0.5(–1) mm, blanquecinas; cuello distinguible, castaño, glabro a piloso, más manifiesto hacia los márgenes; láminas lineares, de 5–23(–32) × 0.3–0.5 cm, predominantemente basales, rectas o falcadas, conduplicadas en la base y planas hacia el ápice, aquilladas, glabras o pilosas, la cara abaxial densamente vilosa, la adaxial esparcidamente pilosa, de base angosta continuándose imperceptiblemente con la vaina, ápice subagudo a obtuso, márgenes hispídulos a escabriúsculos, pestañosos hacia la porción basal. Inflorescencias terminales y axilares, de 8–15 × 2–4 cm, exertas; 1–2 pedúnculos naciendo del último nudo caulinar, de 18–40 cm, cilíndricos, con surco lateral conspicuo, glabros, pajizos; eje principal cilíndrico-anguloso, de 0–3 cm, glabro; racimos (2)3–7(–9), ascendentes, divergentes, alternos, los superiores aproximados a conjugados; raquis de los racimos triquetro, de (5.5–)7.5–10.5(–16) cm × 0.4–0.7 mm, glabro o esparcidamente piloso, con pelitos cortos, los márgenes escabriúsculos; pulvínulos glabros a glabrescentes, con pelos cortos blanquecinos; pedicelos aplanados, de 0.1–0.2 mm, glabros. Espiguillas elipsoides, de (1.5–)1.7–2 × 0.6–0.8 mm, glabras o glabrescentes, con escasos pelos entre los espacios internervales, ápice agudo a subagudo, pajizas a ocreáceas; gluma superior y lema inferior subiguales, del mismo largo que el antecio superior; gluma superior tan larga como la espiguilla, membranáceo-hialina, 2-nervia, nervio medio ausente; lema inferior glumiforme, 2-nervia; antecio superior elipsoide, de 1.6–1.9 × 0.6–0.7 mm, de ápice agudo, finamente papiloso, glabro, castaño, brillante, pajizo en el ápice y la base; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, ca. 0.2 mm; estambres 3, anteras de 1–1.1 mm, purpúreas. Cariopsis elipsoide de 1.4–1.5 × ca. 0.7 mm, pajiza; hilo elíptico a obovoide, subbasal; embrión 1/2 del largo de la cariopsis.

Hábitat y distribución. *Axonopus cuatrecasasii* es una especie sudamericana que crece en Venezuela (Black, 1963: 147), Colombia (Black, 1963: 147) y Bolivia (Dpto. Santa Cruz). La especie crece en sabanas, en suelos arenosos, bien drenados, entre los 100 y los 1000 m.s.n.m.

Discusión. *Axonopus cuatrecasasii* pertenece a la serie *Suffulti* por tener gluma superior y lema inferior ausentes, o poco manifiestos y antecio superior castaño. La especie se caracteriza por incluir plantas cespitosas, con cañas estoloníferas que arraigan en los nudos basales, originando nuevas plantas. *Axonopus cuatrecasasii* es afín a *A. argentinus*, distinguiéndose esta última por incluir plantas cespitosas con rizomas manifiestos (vs. plantas estoloníferas con rizomas cortos) y pedicelos pilosos (vs. pedicelos glabros). Para una mayor aclaración de la variación morfológica y sinonimia véase Cialdella et al. (2006).

Material adicional examinado. BOLIVIA. **Santa Cruz:** Chiquitos, Ea. San Ignacio, 22 km N of San José, *Killeen 1725* (CTES, F, LPB, SI, US); Prov. Warnes, Aeropuerto

Int. De Viru Viru, a 17 km de la ciudad de Santa Cruz, *Menacho et al. 333* (CTES, MO, USZ); Prov. Andrés Ibáñez, zona sur de la ciudad de Santa Cruz, Av. Palmar a 10 km del centro de la ciudad, *Mostacedo 238* (MO, USZ).

12. Axonopus equitans Hitchc. & Chase, Contr. U.S. Natl. Herb. 18(7): 301. 1917. TIPO: [Trinidad.] Trinidad y Tobago. Fort George Rd., Port of Spain [Port-of-Spain], 27 nov. 1912, *A. S. Hitchcock 9988* (holotipo, US 865560!; isotipos, F 573020!, F foto en SI!, US fragm. en SI!).

Axonopus oteroi G. A. Black, Advancing Frontiers Pl. Sci. 5: 126. 1963. TIPO: Brasil. Paraná: Guairá (Salto das Sete Quédas), 7 abr. 1939, *J. Ramos de Otero 273* (holotipo, US 1869758!, US foto en SI!; isotipo, US fragm. en SI!).

Plantas perennes, cespitosas, cortamente rizomatosas; cañas erectas, de 50–100 cm, 2–4 mm diám., lateralmente comprimidas; entrenudos 1–3, de 5–24 cm, estriados, pajizos, glabros; nudos barbados, con pelos castaños. Vainas predominantemente basales, de aspecto iridáceo, de 5–35 cm, glabras a pilosas, aquilladas, con los márgenes membranáceos; lígulas membranáceo-ciliadas, de 0.9–1.4 mm; cuello distinguible, glabro a piloso, castaño; láminas linear-lanceoladas, de 5–32 × 0.5–1.2 cm, planas, glabras a pilosas en ambas caras o más densamente hacia la base de la cara adaxial, de base angostada y ápice agudo a subagudo, en ocasiones bífido, los márgenes escabriúsculos. Inflorescencias terminales y axilares de 12–24 × 2–4.5 cm, laxas, exertas; 1–2 pedúnculos naciendo del último nudo caulinar, hasta de 35 cm, cilíndricos, estriados, glabros; eje principal anguloso, de 3–8 cm, con 4–7 racimos ascendentes, divergentes, alternos, los superiores aproximados a conjugados; raquis de los racimos triquetro, de 50–160 × 0.3–0.5 mm, glabro, de bordes escabriúsculos; pulvínulos pilosos; pedicelos de 0.3–0.5 mm, escabriúsculos. Espiguillas elipsoides a ovoides, de 2.3–2.6 × 0.8–1.2 mm, de ápice obtuso, pajizas a verdosas o con tintes purpúreos, con pelos diminutos, blanquecinos, adpresos, distribuidos longitudinalmente entre los nervios; gluma superior y lema inferior subiguales, del mismo tamaño que el antecio superior o 0.1–0.4 mm más largas; gluma superior de 2.3–2.6 mm, membranácea, 5–7-nervia, los nervios prominentes y escabriúsculos hacia el ápice; lema inferior glumiforme, tan larga como la gluma superior o hasta 0.1 mm más corta, 5-nervia; antecio superior elipsoide, de 2.1–2.2 × 0.7–1.1 mm, pajizo, finamente papiloso, de ápice agudo a subagudo, con un mechón de pelos cortos, blanquecinos; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, de 0.3–0.4 mm, membranáceas, cuneadas; estambres 3, anteras de 1.7–2.1 mm, purpúreas. Cariopsis no vista.

Hábitat y distribución. *Axonopus equitans* crece en el norte de Sudamérica, en Surinam (Judziewicz, 1990: 98), Guayana Francesa (Judziewicz, 1990: 98), Trinidad y Tobago (espécimen tipo de *A. equitans*), y Venezuela hasta el sudeste de Brasil (Paraná, espécimen tipo de *A. oteroi*). Es un taxón que se encuentra en bordes de bosques en galería, sobre suelos rocosos, arenosos y en sabanas húmedas.

Discusión. *Axonopus equitans*, perteneciente a la serie *Barbigeri*, se caracteriza por tener plantas que no sobrepasan los 100 cm de alto, vainas basales de aspecto iridáceo (equitantes, conduplicadas, superpuestas y fuertemente comprimidas lateralmente), láminas linear-lanceoladas, hasta de 1.2 cm de ancho, e inflorescencias laxas, con cuatro a siete racimos. *Axonopus equitans* es morfológicamente afín a *A. pubivaginatus* Henrard, especie que crece en Colombia, norte de Brasil, Guayana Francesa, Guyana y Surinam, la que posee un número mayor de racimos, de cinco a veinte (vs. cuatro a siete); el hecho de no existir otros caracteres diagnósticos podría inferir que ambas especies sean coespecíficas, lo que debe confirmarse con un análisis de un mayor número de especimenes de ambos taxones.

Black (1963) al describir *Axonopus oteroi* señala su afinidad morfológica con *A. equitans*, y la distinguió por la pilosidad del follaje y el color de las glumas, caracteres que son variables dentro de los materiales tipo analizados, y por ende de poca relevancia para mantener a ambas entidades como taxones independientes. Además, este autor señala que en *A. equitans* las vainas basales se disponen equitantes, mientras que en *A. oteroi* son no equitantes. El análisis del ejemplar tipo depositado en US de *A. oteroi* permitió observar que su base se encuentra raleada de hojas y solo posee dos hojas y varias hojas cortadas; sin embargo se puede observar que las bases de las vainas son fuertementes comprimidas y aquilladas como se observa en *A. equitans*. Por las razones expuestas se considera a *A. oteroi* bajo la sinonimia de la especie.

Material adicional examinado. VENEZUELA. **Amazonas:** Río Casiquiare, near L bank of Caño Duquiapo, 2 km above Solano, *Wurdack & Adderley 43382* (NY).

13. Axonopus fissifolius (Raddi) Kuhlm., Relat. Comiss. Linhas Telegr. Estratég. Matto Grosso Amazonas 67(11): 87. 1922. Basiónimo: *Paspalum fissifolium* Raddi, Agrostogr. Bras. [Raddi] 26. 1823, como "*Paspalus fissifolius*". *Axonopus*

fissifolius (Raddi) Chase, J. Wash. Acad. Sci. 13(9): 172. 1923, nom. illeg. superfl. TIPO: Brasil. Rio de Janeiro: Guanabara, s.d., *G. Raddi s.n.* (holotipo, PI no visto; isotipos, BM 678791!, FI!, FI fragm. en BAA 313!, G!, PI fragm. en US 2766195!).

Paspalum compressum (Sw.) P. Beauv. var. *arenarium* Bertoni, Anales Ci. Parag. 2: 153. 1918. TIPO: Paraguay-Argentina. s. loc., 19 oct. 1908, *M. Bertoni 4866* (holotipo, W no visto; isotipo, W fragm. en US 1298737!).

Axonopus affinis Chase, J. Wash. Acad. Sci. 28: 180, fig. 2. 1938. TIPO: Estados Unidos de América. Mississippi: Waynesboro, 2 oct. 1896, *T. H. Kearney Jr. 175* (holotipo, US 928710!; isotipos, BM no visto, BM foto en MO!, GH no visto, MO 2875215!, US 740968!).

Axonopus fissifolius var. *coronatus* G. A. Black, Advancing Frontiers Pl. Sci. 5: 58. 1963. TIPO: Brasil. Minas Gerais: Diamantina, Serra de San Antonio, 1200–1300 m, 27–30 dic. 1929, *A. Chase 10406* (holotipo, US!, US foto en SI!; isotipo, MO 1002561!, MO fragm. en SI!).

Plantas perennes, ligeramente cespitosas, estoloníferas, con largos estolones arraigados en los nudos; cañas erectas o decumbentes, de 10–45 cm × 1.5–2.5 mm diám., comprimidas; entrenudos basales cortos, los superiores de 4–16 cm; nudos castaños, glabros o ralamente pilosos. Vainas de 3–18 cm, las inferiores fasciculadas, las superiores distanciadas, aquilladas, lateralmente comprimidas, glabras, los márgenes membranáceos, glabros o en ocasiones pestañosos hacia la porción distal; lígulas membranáceo-ciliadas, de 0.3–0.5 mm; cuello distinguible, glabro; láminas lineares, de 3–23 × 0.2–0.4(–0.5) cm, rectas a falcadas, planas a conduplicadas, glabras, en ocasiones esparcidamente pilosas en ambas caras o solo sobre la cara adaxial, de base angosta, continuándose imperceptiblemente con la vaina, ápice obtuso, algunas veces bífido, los márgenes escabriúsculos, glabros, los inferiores a veces pestañosos. Inflorescencias terminales y axilares de 3–8 × 0.5–4 cm; 1–4 pedúnculos naciendo del último nudo caulinar, hasta de 30 cm × 0.5 mm, surcado, glabro; eje principal 0–2 cm, anguloso, glabro; racimos 2–3(–6), conjugados a subdigitados, ascendentes, divergentes; raquis de los racimos triquetro, de 30–100 × 0.3–0.5 mm, glabro, los márgenes escabriúsculos; pulvínulos esparcidamente pilosos; pedicelos de 0.3–0.5 mm, lisos o escabriúsculos, comúnmente más angostos que la base de la espiguilla. Espiguillas elipsoides, de 1.5–1.8(–2) × 0.4–0.6 mm, de ápice agudo, pajizas, glabras a esparcidamente pilosas, con pelos cortos blanquecinos en la base, ápice o dispuestos a lo largo de los nervios marginales; gluma superior y lema inferior subiguales, del mismo tamaño que el antecio superior o hasta 0.3 mm mayores; gluma superior de 1.5–1.8(–2) mm, 2–4(5)-nervia, usualmente el nervio medio ausente; lema inferior glumiforme, 2–4(5)-nervia; antecio superior elipsoide, de 1.4–1.8 × 0.4–0.5 mm, pajizo, finamente papiloso, con el ápice obtuso, glabro o cortamente piloso hacia el ápice; pálea de similar textura y ornamentación que la lema, glabra; estambres 3, ca. 1 mm. Cariopsis elipsoide, de 1.2 × 0.4 mm, hilo oblongo, subbasal; embrión un poco menor de 1/2 del tamaño de la cariopsis.

Hábitat y distribución. *Axonopus fissifolius* es una especie de amplia distribución, hallándose desde el sudeste de los Estados Unidos de América hasta Bolivia y centro de Argentina, Paraguay y Uruguay. Introducida en el Viejo Mundo en Europa e Islas del Pacífico (Giraldo-Cañas, 2008b: 305). Esta especie crece en campos bajos, inundables, o en barrancas arenosas, formando céspedes, entre el nivel del mar y los 1500 m.s.n.m. Es frecuentemente utilizada como planta forrajera y para céspedes en diferentes ambientes.

Nombres vulgares. "Kapi' ipe sa' yju" (Paraguay, Morrone et al., 1994: 42); "grama-jesuítica", "grama-tubarão", "grama misionera", "grama-tapete" (Brasil, Smith et al., 1982: 1118).

Números cromosómicos. Se han citado, tal como ocurre a menudo en *Axonopus compressus*, varios niveles de ploidía en *A. fissifolius*, entre los que se pueden citar: $n = 20$ (Davidse & Pohl, 1972: 274, sub *A. affinis* Chase; Hickenbick et al., 1975: 188 sub *A. fissifolius* (Raddi) Kuhlm.); $n = 30$ (Davidse & Pohl, 1978: 641 sub *A. fissifolius*); $n = 40$ (Hickenbick et al., 1975: 188 sub *A. affinis*); $2n = 20$ (Gould & Soderstrom, 1967: 677 sub *A. affinis*; Norrmann et al., 1994: 769 sub *A. fissifolius*); $2n = 80$ (Gould & Soderstrom, 1970: 1634 sub *A. affinis*; Gould & Soderstrom, 1974: 1082 sub *A. affinis*).

Discusión. *Axonopus fissifolius* pertenece a la serie *Axonopus* por tener antecios claros, pajizos, gluma superior con nervio medio usualmente faltante y ápice de las láminas obtuso a agudo, no setáceo. Dentro de esta serie, *A. fissifolius* es morfológicamente afín a *A. compressus* (véase observaciones bajo esta última especie).

Black (1963) describe *Axonopus fissifolius* var. *coronatus* y la distingue de la variedad tipo por poseer inflorescencias con dos a 12 racimos, usualmente cuatro o más. El análisis del material tipo *Chase 10406* permitió determinar que posee inflorescencias con dos a seis racimos, y posiblemente la cita de doce racimos se debe a que varias inflorescencias, terminales y axilares que nacen del último nudo caulinar, se hallan parcialmente exertas en la última

vaina foliar confundiéndose como una única inflorescencia. Por esta razón se considera a la variedad *coronatus* en la sinonimia de *A. fissifolius*.

Axonopus affinis, originalmente descripta para América del Norte (Chase, 1938), ha sido reconocida como una especie diferente y relacionada con *A. fissifolius* (Black, 1963; Valls et al., 2001); esta especie fue diferenciada por presentar láminas más anchas (de 0.4–0.8 cm) y espiguillas de 1.9–2.2 mm, mientras que estos autores caracterizaron a *A. fissifolius* por tener láminas de 0.2–0.4 cm de ancho y espiguillas de 1.6–1.8 mm de largo. El análisis de abundante material de herbario ha permitido observar una marcada variación en los caracteres anteriormente mencionados, tanto en ejemplares diferentes como en un mismo ejemplar, como por ejemplo en *Fredholm 5255*, *Crovetto 2209*, *Herbert 20777*, *Montes 102*, *Nicora 2985*, *Rosengurtt B-5409*, *Rosengurtt B-5441* y *Venturi 1708*. Consecuentemente, se considera a *A. affinis* bajo la sinonimia de *A. fissifolius*.

Material adicional examinado. ARGENTINA. **Buenos Aires:** Delta, Ayo. Pay-Carabí, *Calderón 477* (MO, SI). **Chaco:** Dpto. 1° de Mayo, Colonia Benítez, *Schultz 11677* (CTES, F). **Córdoba:** La Fronda, 30 mar. 1942, *Nicora s.n.* (SI-18594). **Corrientes:** Dpto. Concepción, *Pedersen 15144* (CTES, MO, SI). **Entre Ríos:** Dpto. Federación, Ayo. La Virgen, al S de Federación, *Troncoso et al. 2464* (SI); Dpto. Colón, Ayo. Mármol, *Nicora 2985* (SI); sin Dpto., Holt, *Crovetto 2209* (SI); Paraná Guazú, *Herbert 20777* (SI). **Formosa:** Dpto. Patiño, s. loc., feb. 1972, *Insfrán s.n.* (SI). **Jujuy:** Dpto. Dr. Manuel Belgrano, Juan Galán, *Cabrera et al. 27310* (SI). **Misiones:** Dpto. Candelaria, Ruta Prov. 208, 10 km pasando Cerro Corá hacia Cerro Azul, *Morrone et al. 1785* (MO, SI); Loreto, *Montes 102* (SI). **Salta:** Dpto. Orán, 5 km W de Ruta Nac. 50, próx. puente internac. Argentina–Bolivia, *Pensiero & Marino 4550* (MO, SI). **Tucumán:** Racao, *Parodi 10633* (BAA, CTES); Famaillá, La Fronterita, *Venturi 1708* (SI). BOLIVIA. **Beni:** Ballivián, Espiritu, en la zona de influencia del Río Yacuma, *Beck 3225* (LPB, SI). **Chuquisaca:** Pcia. L. Calvo, entrada al Valle Itangua, *Saravia Toledo et al. 11695* (SI). **La Paz:** Nor-Yungas, Polo Polo bei Coroico, *Buchtien 6434* (SI). **Santa Cruz:** Prov. Ñúflo de Chávez, Ea. Viera, 2 km SE Concepción, *Killeen 1624* (CTES, LPB, MO, SI). **Tarija:** Prov. Burnet O'Connor, Salinas, el Mesón, *Lipa 34* (LPB, SI). BRASIL. **Paraná:** Ponta Grossa, junto ao Parque Est. Vila Velha, *Longhi-Wagner et al. 9432* (CTES, SI). **Rio Grande do Sul:** Mun. Rosario do Sul, Rio Santa María, *Krapovickas et al. 22800* (CTES). ESTADOS UNIDOS DE AMÉRICA. **Florida:** *Fredholm 5255* (SI). PARAGUAY. **Alto Paraná:** Irala, *Montes 11083* (CTES). **Amambay:** Parque Nac. Cerro Corá, *Zuloaga & Morrone 7257* (CTES, MO, SI). **Caaguazú:** Caaguazú, *Sparre & Vervoorst 2209* (LIL). **Central:** San Antonio, *Pedersen 7614* (BAA, CTES); Río Paraguay, Bco. San Miguel, *Rosengurtt B-5441* (SI). **Concepción:** Zwischen Rio Apa & Rio Aquidabán, Caballero Cué, *Fiebrig 5003* (F, G, SI). **Cordillera:** San Bernardino, Campichuelo húmedo San Antonio, *Rojas 14234* (BAA, SI). **Guairá:** 17 km al N de Villarica, *Morrone & Pensiero 316* (SI). **Misiones:** 12 km de San Patricio, camino a Ayolas, *Morrone & Pensiero 224* (MO, SI). **Paraguarí:** 2 km al S de Quindy, camino a Caacupú, *Morrone & Pensiero 195* (MO, SI); Ruta Asunción a Encarnación, Km 128, *Rosengurtt B-5409* (SI). **Presidente Hayes:** Chacoí, campo inundable del Río Negro, *Schinini 26752* (G, LIL). **San Pedro:** Primavera, *Woolston 55* (BAA, SI). URUGUAY. **Canelones:** Santa Lucía, *Jackson s.n.* (CTES-214743). **San José:** Barra del Río Santa Lucía, *Rosengurtt B-282* (US).

14. Axonopus flabelliformis Swallen, Bull. Torrey Bot. Club 75: 82. 1948. TIPO: Guyana. Halfway station betw. Wismar & Rockstone, Demerara River, in sandy soil, 30 dic. 1919–ene. 1920, *A. S. Hitchcock 17275* (holotipo, US 1038571!, US foto en SI!).

Axonopus purpurellus Swallen, Bull. Torrey Bot. Club 75: 83. 1948. TIPO: Surinam. Km 68, vic. Sectie O, on wet sandy soil, 19 Oct. 1944, *B. Maguire & G. Stahel 24997* (holotipo, US 171373!, US foto en US 1914999!; isotipos, NY no visto, NY foto en SI!).

Axonopus kaietukensis Swallen, Bull. Torrey Bot. Club 75: 83. 1948. TIPO: Guyana. Kaieteur Savanna, locally frequent, rocky dry ground, 14 May 1944, *B. Maguire & D. B. Fanshawe 23454* (holotipo, US 171387!, US foto en SI!; isotipos, F no visto, NY 346104!).

Axonopus tamayonis Luces, Bol. Soc. Venez. Ci. Nat. 15(80): 21. 1953. TIPO: Venezuela. Bolívar: Gran Sabana, Santa Elena, en el cerro Okurimá, 11 feb. 1946, *F. Tamayo 2747* (holotipo, VEN 93794!, VEN foto en US!; isotipos, F no visto, MO 3116514!, MO fragm. y foto en SI!, US 1910959!, US 3049572!).

Axonopus flabelliformis var. *camporum* G. A. Black, Advancing Frontiers Pl. Sci. 5: 145. 1963. TIPO: Guayana Francesa. Est. Sinnamary to Iracoubo, Km 13, campo, 29 oct. 1954, *G. A. Black & R. M. Klein 54-17390* (holotipo, IAN no visto; isotipos, CAY no visto, US 2303305!, US foto en SI!).

Axonopus flabelliformis var. *decipiens* G. A. Black, Advancing Frontiers Pl. Sci. 5: 146. 1963. TIPO: Surinam. Poika Savanna, 4 jul. 1951, *A. T. Semple 381* (holotipo, US 2184143!).

Plantas perennes, cespitosas, de 0.55–1(–2) m de alto, con rizoma corto y robusto, cubierto por vainas fibrosas; cañas generalmente aplanadas de 2–4 mm diám., simples, longitudinalmente estriadas, glabras, cubiertas por las vainas basales equitantes; nudos castaños, levemente comprimidos, glabros a densamente vilosos. Vainas conspicuamente estriadas, pajizas, glabras a vilosas, con frecuencia más densamente cerca del margen y hacia el cuello, dispuestas en forma notablemente dística, conduplicadas, comprimidas lateralmente, de manera que las láminas quedan dispuestas en 2 hileras, el conjunto de aspecto flabeliforme; lígulas membranáceo-pestaosas, ca. 0.3 mm, castaño-rojizas, con margen blanquecino; cuello indistinguible; láminas lineares de 10–20(–60) × 0.5–0.9 cm, rígidas, dispuestas en la base y porción mediana de las cañas, plegadas en toda su longitud o solamente en la base y planas

hacia el ápice, de ápice subagudo u obtuso, base continua con la vaina, glabras en ambas caras o bien escabriúsculas en la cara adaxial y densamente vilosas en la cara abaxial, con los márgenes lisos, glabros o hispídulos hacia el ápice, o con escasos pelos de 2.5–3 mm cerca de la base o en toda su extensión. Inflorescencias terminales y axilares; 1–3 pedúnculos naciendo del último nudo caulinar, cilíndricos o aplanados, longitudinalemente estriados, glabros; racimos 6–20(–30), los basales en ocasiones ramificados, alternos, levemente distantes entre sí y los apicales simples, más cercanos; raquis de los racimos de 50–150(–200) × (0.3–)0.6–0.8(–1.3) mm, triquetro, hispídulo en toda su superficie, más conspicuamente sobre los ángulos, glabro o con pelos de 1–1.5 mm, situados sobre los ángulos a ambos lados de la base de algunos pedicelos; pedicelos de (0.1–)0.2–1 mm, glabros a pubérulos. Espiguillas elipsoides, de (1.3–)1.6–2.2 × 0.6–0.7 mm, ocráceas; gluma superior de 1.2–1.5(–2.2) mm, generalmente menor que el antecio, obtusa, muy rara vez igual y aguda, glabra o pubescente con algunos pelitos cortos a ambos lados de los nervios, 2-nervia, ocasionalmente 3-nervia; lema inferior de 1.3–2 mm, ligeramente menor o tan larga como el antecio, glabra o pubescente, 2-nervia; antecio superior elipsoide, de 1.6–1.8 × 0.5–0.6 mm, de ápice agudo, finamente papiloso, castaño, poco brillante, glabro, ocasionalmente con escasos y cortos pelitos en su ápice; pálea de igual consistencia y aspecto que la lema, glabra. Cariopsis no vista.

Hábitat y distribución. *Axonopus flabelliformis* es una especie restringida al norte de América del Sur, en Guyana, Guayana Francesa, Surinam y Venezuela, hallándose también en Bolivia en el Dpto. La Paz. Se halla comúnmente en ambientes abiertos, en sabanas sobre suelos arenosos o entre rocas emergentes, entre los 100 y 1768 m.s.n.m.

Número cromosómico. Se conoce hasta el momento un recuento para *Axonopus flabelliformis* de *n* = 10 (Hickenbick et al., 1975: 189, sub *A. flabelliformis* var. *camporum* G. A. Black).

Discusión. *Axonopus flabelliformis* es un miembro de la serie *Suffulti* por poseer antecios superiores castaños, gluma superior con nervio medio ausente o poco manifiesto. Esta especie es fácilmente reconocible por la disposición marcadamente equitante de sus vainas basales. Comparte este carácter con *A. suffultus*, distinguiéndose esta última especie por tener vainas glaucas y láminas predominantemente basales (vs. vainas pajizas y láminas distribuidas regularmente a lo largo de las cañas) y espiguillas con la gluma superior de igual largo, o levemente más larga, que el antecio superior (vs. gluma superior usualmente más corta que el antecio superior, dejando expuesto el dorso del antecio).

Tal como indicaron previamente Anton (1982) y Judziewicz (1990), *Axonopus flabelliformis* es marcadamente polimorfa en cuanto a la pilosidad de las vainas, de los raquis y de las espiguillas. Para una detallada descripción de la variación morfológica y sinonimia véase Cialdella et al. (2006).

Material adicional examinado. BOLIVIA. **La Paz:** Prov. Tamayo, near Apolo, *Smith 1000* (NY); Prov. Larecaja, San Carlos, San José, Mapiri Region, *Buchtien 12* (BAA, MO); Prov. Franz Tamayo, Senda Apolo–San José de Uchupiamonas a media hora antes de llegar a Naranjai, *Miranda et al. 732* (LPB); Apolo, 57 km hacia Charasani pasando Correo, camp. Calabatea, *Beck 18511* (LPB).

15. Axonopus herzogii (Hack.) Hitchc., Contr. U.S. Natl. Herb. 24(8): 431. 1927. Basiónimo: *Paspalum herzogii* Hack., Repert. Spec. Nov. Regni Veg. 7: 50. 1909. TIPO: Bolivia. Santa Cruz: Santiago de Chiquitos, Cerro San Miserate, mayo 1905, *T. Herzog 866* (holotipo, W no visto; isotipos, W fragm. ex SI!, W fragm. ex US 2855300!). Figura 3.

Plantas perennes, cespitosas; cañas erectas, de 40–90 cm de alto, 1.3–2.5 mm diám., comprimidas; entrenudos 2–5 de 3.5–22 cm, estriados, glabros, pajizos; nudos glabros a ralamente pilosos, castaños. Vainas predominentemente basales, de 4–13 cm, flabeladas hacia la porción basal, generalmente más largas que los entrenudos, glabras, aquilladas, los márgenes membranáceos; las vainas superiores de 12–30 cm; lígulas membranáceo-pestañosas, membrana breve de 0.2–0.25 mm, porción pilosa con pelos blanquecinos de 0.3–0.4 mm de largo; cuello indistinguible, glabro; láminas lineares de 4–25 × 0.3–0.5 cm, conduplicadas, glabras, de base angosta continuándose imperceptiblemente con la vaina, de ápice subagudo a obtuso, los márgenes membranáceos, cortamente pestañosos hacia la base. Inflorescencias terminales de 6–12 × 1–2 cm, exertas; pedúnculos hasta de 35 cm, filiformes, ligeramente estriados, glabros; eje principal de 0–1.5 cm; racimos 2–7, ascendentes, subdigitados, aproximados a conjugados; raquis de los racimos triquetro, de 40–80(–100) × 0.4–0.5 mm, ondulado, los márgenes escabriúsculos, densamente pestañosos, con pelos dorados, de base tuberculada; pedicelos de 0.2–0.4 mm, pilosos, con un mechón de 5–10 pelos tuberculados, dorados, asociados a la base, hasta de 3 mm. Espiguillas elipsoides, de 2.1–2.5 × 0.6–0.8 mm, de ápice agudo, pajizas a castañas o con tintes

Figura 3. *Axonopus herzogii* (Hack.) Hitchc. —A. Hábito. —B. Detalle de la lígula. —C. Ápice de la lámina. —D. Porción del raquis de los racimos con espiguillas, vista ventral. —E. Porción del raquis con espiguillas, vista dorsal. —F. Espiguilla, vista del lado de la gluma superior. —G. Espiguilla, vista del lado de la lema inferior. —H. Antecio superior, vista dorsal mostrando la lema superior. —I. Antecio superior, vista ventral mostrando la pálea superior. —J. Pálea superior, lodículas y estambres (*Killeen & Wellens 6627*, SI).

purpúreos, pilosas en la base e hirsutas en el dorso; gluma superior y lema inferior subiguales, tan largas como la espiguilla; gluma superior con pelos blanquecinos, de base tuberculada, hasta de 3 mm alternando con pelos simples, distribuidos en los espacios internervales, 5-nervia, con nervios prominentes; lema inferior glumiforme, papilosa-pilosa, 3–5-nervia; antecio superior largamente elipsoide, de 1.9–2.2 × 0.5–0.7 mm, castaño oscuro, pajizo en el ápice y en la base, 0.1–0.2 mm más corto que la espiguilla, finamente papiloso, de ápice agudo, piloso, con un mechón de pelos blanquecinos; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, de 0.20–0.25 mm, membranáceas, cuneadas; estambres 2, anteras de 1.2–1.3 mm, purpúreas. Cariopsis no vista.

Hábitat y distribución. *Axonopus herzogii* es una especie sudamericana restringida a Brasil, en los estados de Rondônia, Mato Grosso y en zonas adyacentes de Bolivia, en los departamentos La Paz y Santa Cruz. Esta especie se encuentra en sabanas y afloramientos rocosos entre los 170 y 1000 m.s.n.m.

Discusión. *Axonopus herzogii* pertenece a la sección *Lappagopsis*, la que se caracteriza por incluir especies con raquis piloso y gluma superior y lema inferior papiloso-pilosas, con pelos blanquecinos de base tuberculada; a su vez, la especie comparte con la sección *Cabrera* el poseer antecios superior castaño-oscuros. *Axonopus herzogii* es morfológicamente afín a *A. brasiliensis*, distinguiéndose *A. herzogii* por tener vainas flabeladas en la base (vs. láminas no flabeladas), láminas de ápice redondeado (vs. láminas de ápice agudo), y pedicelos pilosos, asociados a un mechón de pelos dorados, rígidos, de base tuberculada, dispuestos de forma flabelada (vs. pedicelos pilosos solo hacia la base, escabriúsculos y sin un mechón de pelos dorados, rígidos). La presencia de un denso mechón de pelos rígidos, papilosos, dorados, en la base de los pedicelos y antecio superior de color castaño oscuro a la madurez, relaciona a *A. herzogii* con las especies incluídas bajo la sección *Cabrera*, distinguiéndose estas últimas por tener la gluma superior y la lema inferior glabras o esparcidamente pilosas, con pelos delicados cuando presentes, sin base tuberculada.

Material adicional examinado. BOLIVIA. **La Paz:** Prov. Abel Iturralde, Parque Nac. Madidi, Pampas del Heath, al lado del Río Heath, *Gonzales et al. 4459* (LPB, SI). **Santa Cruz:** Prov. Chiquitos, S Slopes of Serrania de Santiago, 5–10 km E of town of Santiago, *Daly et al. 2177* (LPB, MO, SI), 5 km N of Santiago de Chiquitos, near the Arches, *Cutler 7018* (F); Prov. Velasco, Parque Nac. Noel Kempff Mercado, Camp. Laja, *Killeen et al. 7471* (MO, USZ), Reserva For. Bajo Paraguá, Pampa Grande, *Killeen & Wellens 6627* (SI). BRASIL. **Mato Grosso:** Pimenta Bueno to Riozinho, *Kuhlmann 1722* (IAN, RB). **Rondônia:** Guajará–Mirim, estrada do Palheta, *Cordeiro 905* (MO).

16. Axonopus hirsutus G. A. Black, Advancing Frontiers Pl. Sci. 5: 55. 1963. TIPO: Bolivia. Santa Cruz: Portachuelo, s.d., *J. Steinbach in Hb. Osten 14598* [sic, *14958*] (holotipo, US 1297197!; isotipos, GH no visto, IAN no visto, R no visto, US 1297198!).

Plantas perennes, fuertemente estoloníferas; cañas erectas a geniculadas, de 20–40 cm de alto, 1.6–1.9 mm diám., comprimidas; entrenudos 2–4, de 4–9 cm, con surco lateral conspicuo, pajizos; nudos densamente pilosos, castaños. Vainas principalmente basales, de 20–50 × 3–5 mm, glabras, estriadas, con los márgenes membranáceo-pilosos, más densos hacia la porción distal; vainas superiores de 8–13 cm; lígulas membranáceo-ciliadas, de 0.3–0.4 mm; cuello levemente distinguible; láminas linear-lanceoladas, de 3–20 × 0.2–0.5 cm, planas a conduplicadas, densamente pilosas en ambas caras, con pelos de base tuberculada, base angostada, continuándose imperceptiblemente con la vaina, ápice subagudo a obtuso, los márgenes pestañosos hacia la porción basal y escabriúsculos hacia el ápice. Inflorescencias terminales y axilares, de 6–8 × 1–3 cm, exertas; 1(2) pedúnculos naciendo del último nudo caulinar, hasta de 26 cm, filiformes, glabros, con uno de los lados surcado; eje principal anguloso, de 12–20 × 0.5–0.6 mm; racimos 3–4, subdigitados, ascendentes, divergentes, alternos, los superiores aproximados a conjugados; raquis de los racimos triquetro, de 50–80 × ca. 0.5 mm, glabro, bordes escabrosos; pedicelos ca. 0.1 mm, glabros, escabrosos. Espiguillas elipsoides, de 1.6–2 × 0.6–0.7 mm, de ápice obtuso a subagudo, pajizas o con tintes violáceos, glabras a cortamente pilosas, con pelos adpresos entre los nervios; gluma inferior y lema superior subiguales, tan largas como el antecio superior; gluma superior de 1.6–2 mm, membranácea, 2–4-nervia, el nervio medio ausente; lema inferior glumiforme, 2–4-nervia; antecio superior elipsoide, de 1.6–1.9 × ca. 0.6 mm, pajizo, finamente papiloso, de ápice obtuso, con un mechón de pelos cortos, blanquecinos; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, ca. 0.2 mm; estambres 3, anteras de 0.9–1 mm. Cariopsis elipsoide, de 1.4 × 0.6 mm; hilo elíptico; embrión ca. 1/2 del largo de la cariopsis.

Hábitat y distribución. *Axonopus hirsutus* está restringida al estado de Mato Grosso en Brasil y zonas aledañas del departamento Santa Cruz en Bolivia.

Esta especie se encuentra en sabanas húmedas, entre 400 y 500 m.s.n.m.

Discusión. *Axonopus hirsutus* es morfológicamente afín a *A. fissifolius*, distinguiéndose de esta última por tener vainas y láminas papiloso-pilosas (vs. vainas y láminas glabras, ocasionalmente esparcidamente pilosas en la última especie). También es afín a *A. boliviensis*, especie de la que se separa por su hábito perenne, siendo las plantas fuertemente estoloníferas (vs. plantas anuales, cespitosas y sin estolones en *A. boliviensis*). Estos caracteres permitieron concluir que *Renvoize & Cope 3943*, originalmente citado como paratipo de *A. boliviensis* (Renvoize, 1998), es en realidad *A. hirsutus*.

Material adicional examinado. BOLIVIA. **Santa Cruz:** 50 km S Santa Cruz, *Renvoize & Cope 3943* (LPB, MO, SI); Prov. Andrés Ibáñez, Las Lomas de Arena, 5 km E of Palmasola, *Killeen 2297* (LPB, MO, SI, USZ), 10 km E of YPFB refinery, *Killeen 1576* (CTES). BRASIL. **Mato Grosso:** Maria Molina (José Bonifacio), *Kuhlmann 1712* (IAN).

17. Axonopus iridifolius (Poepp.) G. A. Black, Advancing Frontiers Pl. Sci. 5: 125. 1963. Basiónimo: *Paspalum iridifolium* Poepp., Reise Chile 2: 324. 1836. TIPO: Perú. "in collibus sylvaticis ad Cochero", 1828, *E. F. Poeppig 24* (holotipo, W no visto; isotipos, LE TRIN 0475-01!, LE foto y fragm. en SI!, LE fragm. en US 2855290!, US 2855290!, US foto y fragm. en SI!).

Plantas perennes, robustas, cespitosas; cañas erectas, de 50–120 cm de alto, 5–8 mm diám., cilíndricas a comprimidas; entrenudos 3–8, de 7–26 cm, estriados, levemente surcados, pajizos, glabros; nudos glabros a barbados, castaños. Vainas de 7–35 cm, lateralmente comprimidas, glabras, aquilladas, los márgenes membranáceos, glabros a pestañosos hacia la porción superior; lígulas membranáceo-ciliadas, de 1–1.5 mm; cuello levemente distinguible, glabro; láminas lanceoladas, de (6–)10–30 × 0.5–2 cm, planas, glabras a esparcidamente pilosas, de base redondeada a atenuada, ápice obtuso o agudo, los márgenes membranáceos, escabriúsculos. Inflorescencias terminales o axilares, laxas, de 13–30 × 3–5 cm, exertas; 1–2 pedúnculos, de 13–35 cm × 0.8–1.6 mm, cilíndricos a angulosos, escabrosos; racimos 6–20, ascendentes, divergentes, alternos, subopuestos o subverticilados; raquis de los racimos triquetro, de 80–200 × 0.3–0.5 mm, glabro a esparcidamente piloso, los márgenes escabriúsculos; pedicelos de 0.2–0.4 mm, glabros o finamente pubescentes, escabriúsculos. Espiguillas elipsoides, de 1.9–2.5 × 0.6–0.8 mm, de ápice subagudo, glabrescentes a pubérulas, con pelos adpresos, blanquecinos, delicados, dispuestos en las zonas internervales, pajizas o con tintes purpúreos; gluma inferior y lema superior subiguales, 0–0.3 mm mayores que el antecio superior; gluma superior de 2.1–2.5 mm, membranácea, 5(–7)-nervia, con nervios prominentes, escábridos hacia el ápice; lema inferior glumiforme, 5-nervia; antecio superior elipsoide, de 1.8–2.1 × 0.6–0.8 mm, de ápice subagudo, pajizo, finamente papiloso, glabro o con unos pocos pelos cortos, delicados y blanquecinos en el ápice; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, de 0.15–0.3 mm, membranáceas, cuneadas; estambres 3, anteras de 1–1.3 mm. Cariopsis no vista.

Hábitat y distribución. *Axonopus iridifolius* es una especie sudamericana de amplia distribución a lo largo de los Andes, hallándose en Venezuela, Perú y Bolivia en los departamentos La Paz y Santa Cruz. Esta especie crece en bordes de caminos, campos abandonados, en suelos perturbados y en borde de bosques; se la encuentra entre los 800 y 1600 m.s.n.m.

Discusión. *Axonopus iridifolius* pertenece a la serie *Barbigeri* por tener espiguillas con gluma superior y lema inferior con nervios marcados, incluyendo el nervio medio. Esta especie es morfológicamente afín a *A. scoparius*, distinguiéndose de esta última por incluir plantas de 0.5–1.2 m de alto (vs. plantas de 0.7–2 m en *A. scoparius*), láminas de (6–)10–30 × 0.5–2 cm (vs. láminas de 15–50 × 0.7–4 cm), región ligular levemente distinguible (vs. marcadamente distinguible), inflorescencias pauciracemosas con seis a 20 racimos (vs. inflorescencias multiracemosas con 10 a más de 100 racimos) y espiguillas de 1.9–2.5 mm (vs. espiguillas de 2.3–2.8 mm en *A. scoparius*).

Material adicional examinado. BOLIVIA. **La Paz:** Prov. Nor Yungas, Coroico, 10 km hacia Coripata bajando la Comun. Concepción, 600 km hacia NE, *Beck & Rúgolo 19935* (K, LPB, SI), Caranavi to Coroico, 26 km from Coroico, *Renvoize 4740* (LPB, MO). **Santa Cruz:** ca. 5–6 km along rd. from Bermejo to Los Volcanes, *Wood 10805* (LPB). VENEZUELA. **Aragua:** 12 km S of Alto de Choroní, *Davidse 13076* (MO).

18. Axonopus kuhlmannii G. A. Black, Advancing Frontiers Pl. Sci. 5: 156, tab. 14. 1963. TIPO: Brasil. Mato Grosso: Campo dos Urupás, ene. 1919, *J. G. Kuhlmann 1730* (holotipo, IAN 62429 no visto; isotipos, IAN foto y fragm. en US 2236060!, RB no visto). Figura 4.

Plantas perennes, cespitosas, cortamente rizomatosas; cañas de 55–90 cm de alto, 1.3–3 mm diám., erectas a geniculadas, comprimidas; entrenudos 4–10, de 2–13 cm, lisos, pajizos, glabros; nudos glabros a pilosos, con pelos de 1.2–1.4 mm, blanquecinos, adpresos. Vainas de 2–12 cm, equidistantes entre sí, glabras o pilosas hacia la base, aquilladas, los márgenes membranáceos; vaina superior hasta de 20 cm, lígulas membranáceo-ciliadas, ca. 0.3 mm; cuello indistinguible, glabro; láminas linear-lanceoladas, de 4–35 × 0.2–0.5 cm, conduplicadas, glabras, de base angosta, continuándose imperceptiblemente con la vaina, ápice agudo a acuminado, los márgenes membranáceos, glabros. Inflorescencias terminales y axilares de 6–12 × 0.5–2 cm, exertas; 1–2 pedúnculos naciendo del último nudo caulinar, de 15–35 cm, cilíndricos, lisos, glabros o glabrescentes; eje principal anguloso, de 0–40 × 0.7–0.9 mm, glabro; racimos 2–10, subdigitados, ascendentes, divergentes, los superiores aproximados a conjugados; raquis de los racimos triquetro, de 50–100 × 0.5–0.6 mm, glabro, los márgenes escabrosos; pedicelos de 0.2–0.3 mm, escabrosos. Espiguillas largamente ovoides, de 1.8–2 × 0.6–0.7 mm, pilosas en los márgenes, ápice agudo a subagudo, pajizas; gluma superior y lema inferior subiguales o esta última 0.15–0.2 mm más corta; gluma superior tan larga como la espiguilla, los márgenes pestañosos con pelos pectinados, tuberculados, blanquecinos, hasta de 0.8 mm, 2-nervia, nervio medio ausente; lema inferior glumiforme, glabra, 2-nervia, escabrosa hacia el ápice, en ocasiones el nervio medio presente; antecio superior largamente elipsoide, de 1.6–1.8 × 0.5–0.6 mm, castaño oscuro, pajizo hacia el ápice y la base, finamente papiloso, el ápice agudo y con unos pocos pelos cortos y blanquecinos; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, de 0.15–0.2 mm, membranáceas, cuneadas; estambres 3, anteras de 0.6–0.8 mm. Cariopsis no vista.

Hábitat y distribución. *Axonopus kuhlmannii* crece en Brasil, en los estados de Mato Grosso y Rondônia; aquí se cita por primera vez su presencia en Bolivia, en la provincia de La Paz. La presencia de esta especie en Bolivia no es llamativa, considerando la cercanía entre los estados de Brasil, antes citados, y el departamento La Paz en Bolivia. En ambos países, *A. kuhlmannii* crece en sabanas o en campos húmedos entre 100 y 200 m.s.n.m.

Discusión. *Axonopus kuhlmannii* pertenece a la serie *Fastigiati* G. A. Black por poseer gluma superior largamente ciliada y lema inferior usualmente glabra o esparcidamente pilosa. Esta especie es morfológicamente afín a *A. fastigiatus* (Nees ex Trin.) Kuhlm. por tener ambos taxones espiguillas con la gluma superior largamente pestañosa en los márgenes y con pelos pectinados. *Axonopus fastigiatus* se distingue por tener espiguillas largamente elipsoides, de 3.5–4.8 mm de largo (vs. 1.8–2 mm en *A. kuhlmannii*), gluma superior 4–5-nervia (vs. 2-nervia), antecio superior pajizo (vs. castaño oscuro) e inflorescencias con dos, ocasionalmente uno, racimos conjugados (vs. dos a 10 racimos en *A. kuhlmannii*).

Material adicional examinado. BOLIVIA. **La Paz:** Prov. Abel Iturralde, Luisita, *Haase 627* (SI), P. N. Madidi, Pampas de Heath, lado Río Asunta, *Gonzales et al. 3733* (SI). BRASIL. **Rondônia:** Campo dos Amigos, Bahia do Meio, Rio Guaporé, *Black & Cordeiro 52-14998* (IAN).

19. Axonopus leptostachyus (Flüggé) Hitchc., Contr. U.S. Natl. Herb. 22(6): 471. 1922. Basiónimo: *Paspalum leptostachyum* Flüggé, Gram. Monogr., *Paspalum* 122. 1810, como "*Paspalus leptostachyos*". TIPO: Venezuela. s. loc., s.d., *F. W. H. A. von Humboldt & A. J. A. Bonpland s.n.* (holotipo, B-W!; isotipos, B-W fragm. en US 80079!, US fragm. en SI!).

Axonopus paranaensis Parodi, Revista Argent. Agron. 28(3–4): 111, f. 3. 1961 [1962]. *Axonopus paranaensis* Parodi ex G. A. Black, Advancing Frontiers Pl. Sci. 5: 87. 1963, nom. illeg. superfl. TIPO: Argentina. Misiones: Puerto la Mina, 22 ene. 1922, *L. R. Parodi 4266* (holotipo, BAA!; isotipos, IAN no visto, US 1129071!, US fragm. en SI!).

Plantas perennes, cespitosas, robustas; cañas erectas, de 50–120 cm × 3–6 mm diám., comprimidas; entrenudos 2–5, los basales cortos, los superiores de 10–35 cm, con un lado surcado, pajizos, glabros; nudos glabros o algo pilosos, castaños. Vainas predominantemente basales, formando fascículos, las inferiores de 5–15 cm, comprimidas, aquilladas, glabras, los márgenes membranáceos, ocasionalmente pestañosos hacia la porción apical, con pelos de base tuberculada; vainas superiores hasta de 30 cm; lígulas membranáceo-ciliadas, de 0.15–0.2 mm; cuello distinguible por una delgada línea oscura, glabro; láminas lineares, de 10–60 × 0.6–1.2 cm, planas a conduplicadas, aquilladas, glabras en ambas caras, de base angosta continuándose imperceptiblemente con la vaina, ápice obtuso a subagudo, en ocasiones bífido, los márgenes escabriúsculos. Inflorescencias terminales y axilares de 10–25 × 1–3 cm, cortas a largamente exertas; 1–3 pedúnculos, hasta de 55 cm, filiformes, glabros, surcado; eje principal anguloso, de 30–90 × 0.8–1.2 mm, glabro; racimos 5–20, ascendentes, divergentes, alternos, los superiores aproximados a conjugados;

Figura 4. *Axonopus kuhlmannii* G. A. Black. —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Espiguilla, vista del lado de la gluma superior. —E. Espiguilla, vista del lado de la lema inferior. —F. Antecio superior, vista dorsal mostrando la lema superior. —G. Antecio superior, vista ventral mostrando la pálea superior. —H. Pálea superior, lodículas y filamentos estaminales (*Haase 627*, SI).

raquis de los racimos triquetro, de 10–25 cm × 0.4–0.6 mm, glabro, los márgenes escabriúsculos; pedicelos de 0.4–0.5 mm, glabros, escabriúsculos. Espiguillas elipsoides, de 2.1–2.9(–3.3) × 0.6–0.8 mm, glabras o cortamente pubescentes hacia la base, ápice subagudo, escabriúsculas en los márgenes y el ápice, pajizas o con tintes violáceos; gluma superior y lema inferior subiguales, 0.6–0.8 mm más largas que el antecio superior; gluma superior 2.1–2.9(–3.3) mm, membranácea, 3–5-nervia, con los nervios manifiestos, el central presente; lema inferior glumiforme, 2–3-nervia, con el nervio medio manifiesto; antecio superior elipsoide, de 1.6–2.6 × 0.6–0.9 mm, castaño oscuro en la madurez, finamente papiloso, de ápice obtuso, glabro o con un mechón de pelos blanquecinos; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, de 0.2–0.3 mm, hialinas, conduplicadas; estambres 3, anteras de 0.9–1.1 mm, púrpuras. Cariopsis no vista.

Hábitat y distribución. *Axonopus leptostachyus* se distribuye desde el norte de Sudamérica, en Venezuela, Colombia, Trinidad, las Guyanas y el norte de Brasil (Judziewicz, 1990: 102) hasta Bolivia (Beni, La Paz, Santa Cruz), Paraguay (Itapúa) y norte de Argentina (Chaco, Corrientes, Misiones). La especie habita frecuentemente en lugares bajos e inundables o en orillas de ríos, desde el nivel del mar hasta los 300 m.s.n.m.

Nombres vulgares. "Kapi'i capilla", "kapi'i jesuita" (Paraguay, Morrone et al., 1994: 44).

Número cromosómico. Existe para esta especie un recuento de $n = 40$ (Giraldo-Cañas, 2008a: 44 sub *Axonopus leptostachyus* (Flüggé) Hitchc.).

Discusión. *Axonopus leptostachyus* se distingue morfológicamente de las demás especies del género por incluir plantas robustas que pueden alcanzar más de 1 m de alto, láminas hasta de 60 cm de largo y 1.2 cm de ancho, inflorescencias multiracemosas, hasta de 20 racimos, los cuales pueden alcanzar los 25 cm de largo, antecio superior 0.6–0.9 mm más pequeño que la espiguilla y castaño oscuro a la madurez.

Black (1963) incluyó a *Axonopus leptostachyus* dentro de la serie *Axonopus*. Sin embargo, la especie debe ser tratada bajo la serie *Barbigeri* por tener los nervios de la gluma superior manifiestamente marcados y el nervio medio comúnmente desarrollado, por la cantidad de racimos, el hábito cespitoso y robusto y el tamaño y ápice de la lámina.

Parodi (1961) al describir *Axonopus paranaensis* señala la similitud morfológica de esta especie con *A. leptostachyus*, indicando este autor que esta última se aparta por incluir plantas de mayor tamaño, raquis más largo y glumas pubescentes, 5-nervias. El análisis del material tipo y de ejemplares de herbario permitió determinar que no existen diferencias para tratar a ambos taxones como especies distintas.

Axonopus leptostachyus posee el antecio superior castaño a la madurez, característica morfológica que también se halla presente en las especies incluidas en la serie *Suffulti*. No obstante, las especies de la serie *Suffulti* claramente se distinguen por poseer la gluma superior y lema inferior nervios tenues, estando el nervio medio comúnmente ausente, como así también por ser el raquis de las ramificaciones y los pedicelos generalmente pilosos (Cialdella et al., 2006).

Axonopus longispicus (Döll) Kuhlm. (Kuhlmann, 1922) es una especie que se encuentra en el norte de Sudamérica donde está presente en Colombia, Venezuela, Guyanas, Guayana Francesa y Brasil, en los estados de Amazonas, Mato Grosso y Pará (Giraldo-Cañas, 2008: 132). Esta especie posee espiguillas similares a las presentes en *A. leptostachyus*, con la gluma superior y lema inferior (3–)5-nervias, con los nervios marcados, y antecio superior 0.5–1.5 mm más corto que la espiguilla. *Axonopus longispicus* se separa por tener inflorescencias con menor número de racimos (dos a seis vs. cinco hasta 20) y antecio superior pajizo (vs. castaño oscuro a la madurez en *A. leptostachyus*).

Material adicional examinado. ARGENTINA. **Chaco:** San Fernando, *Pedersen 8708* (CTES). **Corrientes:** Dpto. Goya, 25 km S de Goya, Ea. Aguay, Ayo. Paraná Miní, *Schinini et al. 19324* (BAA, CTES). **Misiones:** Candelaria, Santa Ana, balneario Mun., *Zuloaga et al. 3175* (MO, SI). BOLIVIA. **Beni:** Prov. Ballivián, Espiritu, en la zona de influencia del Río Yacuma, *Beck 5134* (LPB, SI). **La Paz:** Prov. Iturralde, Luisita, *Haase 626* (K, LPB). **Santa Cruz:** Prov. Velasco, camino de San Ignacio de Velasco a Sta. Rosa de la Roca, pasando 2 km Villa Nueva, *Morrone & Belgrano 5075* (CTES, LPB, SI). PARAGUAY. **Itapúa:** Isla Yacyretá, *Jiménez 29* (SI).

20. Axonopus marginatus (Trin.) Chase ex Hitchc., Contr. U.S. Natl. Herb. 17(3): 226. 1913. Basiónimo: *Paspalum marginatum* Trin., Gram. Panic. [Trinius] 90. 1826. *Axonopus marginatus* (Trin.) Kuhlm., Relat. Comiss. Linhas Telegr. Estratég. Matto Grosso Amazonas 67(11): 87. 1922, nom. illeg. superfl. TIPO: Brasil. Minas Gerais: Serra da Lapa [Serra do Cipó], nov. 1824, *G. H. Von Langsdorff s.n.* (holotipo, LE 0490.01!, LE 0490.01 foto en SI!; isotipos, LE 0490.02!, LE 0490.02 foto en SI!, LE fragm. en US 2855812!, LE fragm. en SI!).

Paspalum marginatum Trin. var. *longecilium* Hack., Repert. Spec. Nov. Regni Veg. 7: 370. 1909.

Axonopus longecilius (Hack.) Parodi, Notas Mus. La Plata, Bot. 3(17): 22. 1938. TIPO: Paraguay. Amambay: Sierra de Amambay, Ponta Porá, dic. 1907, *E. Hassler 9746* (*leg. Rojas*) (holotipo, W!; isotipos, G!, W fragm. en BAA 318!, W fragm. en US 2855811!, W fragm. en SI!).

Plantas perennes, cespitosas; cañas de 25–70 cm de alto, 1.8–2.4 mm diám., simples, notoriamente comprimidas; entrenudos 1–2, de 2–15 cm, con un lado surcado, pajizos, glabros a esparcidamente pilosos hacia la porción superior; nudos vilosos. Vainas predominantemente basales, formando fascículos densos, de 2–10 cm, conduplicadas, aquilladas, glabras a híspidas, con pelos tuberculados, los márgenes glabros a pestañosos; vainas superiores de 7–13 cm, distanciadas entre sí; lígulas membranáceo-ciliadas, de 0.2–0.4 mm; cuello indistinguible; láminas lineares, de 4–20 × 0.2–0.4 cm, falcadas, conduplicadas a planas, esparcida a densamente pilosas en ambas caras, con la base angosta continuándose imperceptiblemente con la vaina, de ápice obtuso a subagudo, los márgenes pestañosos. Inflorescencias terminales o axilares, de 4–15 × 0.8–2.5 cm, exertas o subincluidas; 1–2 pedúnculos naciendo del último nudo caulinar, hasta de 30 cm, teretes a subteretes, estriados, glabros a esparcidamente pilosos hacia la porción superior; eje principal anguloso, de 1–3 cm, glabro a híspido; racimos 3–11, subdigitados, ascendentes, divergentes, alternos, las superiores aproximados; raquis de los racimos de 3–12 × 0.4–0.6 cm, glabro, escabroso en los márgenes; pulvínulos cortamente pilosos; pedicelos de 0.15–0.3 mm, glabros, escabriúsculos. Espiguillas elipsoides, de 2.5–3.6 × 1–1.2 mm, de ápice agudo, pajizas o con tintes violáceos, híspidas, con abundantes pelos blanquecinos hasta de 2 mm en la base, blanco-plateados, purpúreos o fuscescentes; gluma superior y lema inferior subiguales, 0.3–0.7 mm más largas que el antecio superior; gluma superior de 2.5–3.6 mm, membranácea, hialina, delicada, 2(–4)-nervia, con el nervio medio ausente; lema inferior glumiforme, 2-nervia, el nervio medio ausente; antecio superior elipsoide, de 2.1–3 × 0.6–1 mm, pajizo, finamente papiloso, de ápice subagudo, con un mechón de pelos tiesos, blanquecinos, hacia el ápice; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, ca. 0.3 mm; estambres 3, anteras de 1.9–2.5 mm. Cariopsis no vista.

Hábitat y distribución. *Axonopus marginatus* habita en el centro y sur de Brasil, en el estado de Paraná, en Bolivia (Beni, La Paz, Potosí y Santa Cruz), en la región oriental de Paraguay (Amambay) y en el noreste de la Argentina (en la provincia de Misiones). Se la encuentra en campos bajos e inundables, en suelos arenosos y en campos sujetos a fuegos periódicos, siendo usual encontrar las bases de las plantas con zonas quemadas, entre el nivel del mar y los 2000 m.s.n.m.

Número cromosómico. Existe para *Axonopus marginatus* un recuento de $2n = 40$ (Gould & Soderstrom, 1967: 677 sub *A. marginatus* (Trin.) Chase ex Hitchc.).

Discusión. *Axonopus marginatus*, miembro de la serie *Axonopus*, se caracteriza por la presencia de vainas principalmente basales formando fascículos densos, conduplicadas, aquilladas, cuello indistinguible, con la base de la lámina continuándose imperceptiblemente con la vaina, espiguillas de 2.5–3.5 mm de largo, densamente híspidas y antecio superior de 2.1–3 mm de largo, 0.3–0.7 mm corto que la espiguilla. *Axonopus marginatus* es morfológicamente afín a *A. purpusii*, apartándose esta última especie por tener las espiguillas insertas oblícuamente en los pedicelos (véase observaciones bajo *A. purpusii*).

Axonopus marginatus posee espiguillas con largos pelos en la base, el ápice y a lo largo de los nervios marginales, siendo la densidad y el color de estos marcadamente variable. Así, se han observado ejemplares que poseen espiguillas con pelos blanco-plateados y esparcidos y otros con espiguillas densamente pilosas, con pelos purpúreos o blanquecinos.

Material adicional examinado. ARGENTINA. **Misiones:** Dpto. Candelaria, Loreto, 8 km E de Loreto, *Morrone et al. 1709* (CTES, MO, SI). BOLIVIA. **Beni:** Yacuma, 96.6 km en el S de Riberalta al E del camino Riberalta–Sta. Rosa, ca. desvío a Cobija, *Hanagarth & Rosales 150* (LPB). **La Paz:** Prov. Nor Yungas, Coroico, *Beck 17852* (K, LPB, SI). **Potosí:** Saavedra, ca. 30–35 km below Charazani in Río Camota valley, on rd. to Apolo, *Wood & Goyder 15427* (LPB). **Santa Cruz:** Prov. Ñúflo de Chávez, Ea. Salta, 10 km S of Concepción, *Killeen 1200* (CTES, F, LPB, MO, SI, USZ). BRASIL. **Paraná:** Camino de Castro a Tibaji, *Morrone & Zuloaga 5380* (SI). PARAGUAY. **Amambay:** Cabecera del Río Aquidabán, Sierra de Amambay, *Rojas 6537* (BAA).

21. Axonopus obtusifolius (Raddi) Chase, J. Wash. Acad. Sci. 13(9): 171. 1923. Basiónimo: *Paspalum obtusifolium* Raddi, Agrostogr. Bras. [Raddi]: 23. 1823. *Anastrophus obtusifolius* (Raddi) Nash, N. Amer. Fl. 17(2): 162. 1912. TIPO: Brasil. Rio de Janeiro: Guanabara, s.d., *G. Raddi s.n.* (holotipo, PI!; isotipos, FI no visto, K no visto, PI fragm. en US-2942535!, PI fragm. en SI!).

Axonopus chaseanus Herter, Revista Sudamer. Bot. 9: 111. 1953. nom. illeg. superfl.

Plantas perennes, estoloníferas, con estolones hasta de 1 m de largo; cañas erectas a geniculadas, de 8–50 cm × 2–3 mm diám., comprimidas, estriadas, pajizas, glabras; nudos 1–3, vilosos, castaños. Vainas predominantemente basales, de 3–7 cm, glabras a pilosas, con los márgenes membranáceos, pestañosos hacia la porción superior; vainas superiores hasta de 20 cm; lígulas membranáceo-ciliadas, cortamente ciliadas en el ápice, de 0.3–0.5 mm; cuello distinguible, piloso, castaño; láminas lanceoladas, de 5–25 × 1–2.3 cm, planas, con prefoliación convoluta, glabras, de base redondeada y ápice obtuso, los márgenes usualmente pestañosos, con pelos de base tuberculada. Inflorescencias terminales y axilares de 4–9 × 1.5–3 cm, exertas o subincluidas en las vainas; 1(2) pedúnculos naciendo del último nudo caulinar, de 10–20 cm, planos a triquetros, con un lado surcado, estriados, glabros; eje principal plano-anguloso, de 0.8–3 cm; racimos 2(3), ascendentes, divergentes, alternos, distanciados entre sí; raquis de los racimos triquetro, de 30–60 × 0.8–0.9 mm, glabro; pedicelos de 0.3–0.4 mm, glabros. Espiguillas elipsoides, de (3.6–)4–5.5 × 1.2–1.5 mm, de ápice agudo, pajizas a verdosas, cortamente pubescentes, con pelos blanquecinos, delicados, distribuidos en la base y entre los nervios; gluma inferior y lema superior subiguales, 1.2–2.5 mm más largas que el antecio superior; gluma superior tan larga como la espiguilla, membranácea, 2–4(5)-nervia, nervio medio, cuando presente, poco manifiesto; lema inferior glumiforme, 2–4(5)-nervia, con el nervio medio usualmente ausente; antecio superior elipsoide, de 2.1–3 × 1.2–1.4 mm, finamente papiloso, de ápice subagudo y con un mechón de pelos blanquecinos; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, de 0.25–0.3 mm; estambres 3, anteras de 0.7–1 mm. Cariopsis no vista.

Hábitat y distribución. *Axonopus obtusifolius* crece en el centro y sur de Brasil (Paraná, Rio Grande do Sul y Santa Catarina) y ha sido introducida en Argentina en la provincia de Misiones. Esta especie habita principalmente en suelos arenosos y húmedos del litoral y en áreas modificadas y perturbadas entre los 200 y 400 m.s.n.m. También es cultivada para césped y forraje (Black, 1963).

Nombres vulgares. "Capin-doce", "grama", "grama-branca", "grama comum", "grama-común-larga", "grama-de-folha-larga", "grama-de-tubarão", "grama-larga", "sempre verde", "sempre-verde-de-folhas-largas" (Brasil, Smith et al., 1982: 1104).

Número cromosómico. Existe para *Axonopus obtusifolius* un recuento de $n = 50$ (Hickenbick et al., 1975: 188 sub *A. obtusifolius* (Raddi) Chase).

Discusión. *Axonopus obtusifolius* pertenece a la serie *Axonopus* y se caracteriza principalmente por formar largos estolones, por sus hojas planas y anchas de ápice y base redondeada, por poseer dos (o tres) racimos que se disponen distanciados entre sí, nunca conjugados, espiguillas de (3.6–)4–5.5 mm y antecio superior 2/3 del tamaño de la espiguilla. Esta especie es morfológicamente afín a *A. compressus*, distinguiéndose esta última por tener los racimos aproximados, los superiores conjugados, y espiguillas menores de 2–2.6(–3) mm de largo (vs. [3.6–]4–5.5 mm de largo en *A. obtusifolius*).

Material adicional examinado. ARGENTINA. **Misiones:** Dpto. Guaraní, Ruta Prov. 2, Reserva Ecol. Prov., *Morrone et al. 722* (CTES, MO, SI). BRASIL. **Paraná:** Serra do Mar, camino de Morretes a Antonina, *Morrone & Zuloaga 5384* (SI). **Rio Grande do Sul:** Terra de Areia, Ruta RS-389, *Rúgolo et al. 1784* (MO, SI). **Santa Catarina:** Río Fortuna, Alto Río Fortuna, *Klein & Bresolini 11329* (F).

22. Axonopus pellitus (Nees ex Trin.) Hitchc. & Chase, Contr. U.S. Natl. Herb. 18(7): 301. 1917.

Basiónimo: *Paspalum pellitum* Nees ex Trin., Gram. Panic. [Trinius] 89. 1826. *Paspalum pellitum* Nees, Fl. Bras. Enum. Pl. 2(1): 29. 1829, como "*Paspalus pellitus*", nom. illeg. superfl. *Paspalum barbatum* Nees var. *pellitum* (Nees ex Trin.) Döll, Fl. Bras. 2(2): 108. 1877. TIPO: Brasil. s. loc., s.d., *F. Sellow s.n.* (holotipo, LE 0507.01!, LE 0507.01 foto en SI!; isotipos, B no visto, B fragm. en BAA-325!, B fragm. en SI!, LE fragm. en US 1258173!, LE fragm. en US 2942521!, LE 0507.02 foto en SI!, US 2855755!, US foto en SI!). Figura 5.

Axonopus swallenii G. A. Black, Advancing Frontiers Pl. Sci. 5: 92, fig. 3m, n. 1963. TIPO: Brasil. Pará: Santarém, 19–26 ene. 1934, *J. R. Swallen 3258* (holotipo, US 1614335!, US foto en SI!; isotipo, US fragm. en SI!).

Plantas perennes, cespitosas, robustas; cañas erguidas, de 50–200 cm de alto, 2.5–10 mm diám.; entrenudos 3–8, hasta de 36 cm, generalmente cilíndricos, glabros; nudos 2–7, usualmente vilosos. Vainas de 10–60 cm, densamente vilosas, con pelos largos, plateados, los márgenes membranáceos, pestañosos; lígulas membranáceo-ciliadas, de 0.3–1 mm; láminas filiformes, de 10–75 × 0.2–0.6 mm, convolutas o planas hacia la porción superior, esparcidamente pilosas a densamente vilosas en toda su superficie, de base angostada y ápice filamentoso, los márgenes escabriúsculos. Inflorescencias termi-

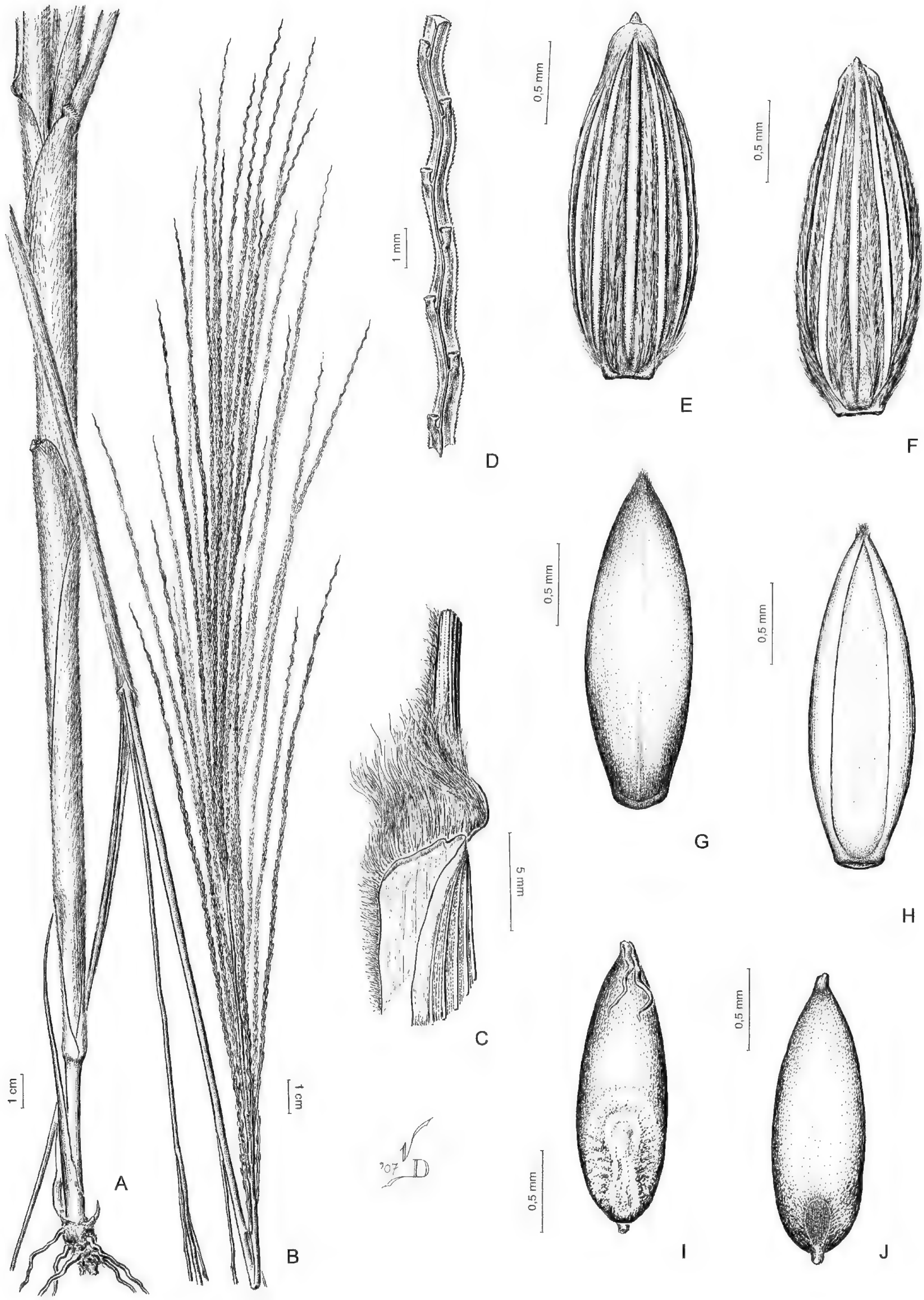

Figura 5. *Axonopus pellitus* (Nees ex Trin.) Hitchc. & Chase. —A. Porción basal de la planta. —B. Detalle de la inflorescencia. —C. Detalle de la lígula. —D. Porción del raquis de los racimos, pedicelos. —E. Espiguilla, vista del lado de la gluma superior. —F. Espiguilla, vista del lado de la lema inferior. —G. Antecio superior, vista dorsal mostrando la lema superior. —H. Antecio superior, vista ventral mostrando la pálea superior. —I. Cariopsis, vista escutelar. —J. Cariopsis, vista hilar (*Filgueiras 3511*, SI).

nales y axilares de 12–40 cm; pedúnculos 1–2, de 30–75 cm, cilíndricos, finamente estriados, glabros; eje principal anguloso, escabroso; racimos 20–50, ascendentes, divergentes, alternos a subverticilados, los superiores aproximados; raquis de los racimos triquetro, de 0.3–0.5 mm, los márgenes escabriúsculos; pulvínulos densamente pilosos; pedicelos triquetros, de 0.3–0.5 mm. Espiguillas elipsoides, de (1.5–) 1.8–2.5 × 0.6–0.8 mm, de ápice agudo a subagudo, pajizas, glabras a glabrescentes, con pelos cortos, delicados, en la base y entre los nervios; gluma superior y lema inferior subiguales, del mismo largo que el antecio superior o 0.2–0.3 mm más largas; gluma superior tan larga como la espiguilla, membranácea, 5-nervia, los nervios manifiestos; lema inferior glumiforme, 5-nervia; antecio superior elipsoide, de (1.5–)1.7–2.4 × 0.5–0.7 mm, pajizo, finamente papiloso, de ápice subagudo, glabro o con un mechón de pelos cortos hacia el ápice; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, ca. 0.2 mm; estambres 3, anteras de 1.4–1.5 mm, purpúreas. Cariopsis no vista.

Hábitat y distribución. *Axonopus pellitus* es una especie endémica del centro y sur de Brasil, donde se encuentra en los estados de Pará y Paraná. Es frecuente en campos abiertos o en áreas montañosas, secas, desde el nivel del mar hasta los 1100 m.s.n.m.

Discusión. *Axonopus pellitus*, miembro de la serie *Barbigeri*, se caracteriza por poseer cañas con nudos y vainas vilosas a densamente vilosas, con pelos largos, plateados, láminas filiformes, hasta de 6 mm de ancho y espiguillas de (1.5–)1.8–2.5 mm. Está estrechamente relacionada a *A. siccus* (Nees) Kuhlm.; esta última especie se separa por tener vainas y láminas glabras a esparcidamente pilosas, cuando pilosas sin pelos plateados (vs. vainas densamente vilosas y láminas esparcida a densamente vilosas, con pelos plateados en *A. pellitus*).

Black (1963) al describir *Axonopus swallenii* la separa de *A. pellitus* por poseer el ápice de las láminas acuminado y rígido y antecio superior glabro. El análisis del material tipo y de ejemplares de herbario permitió determinar que los caracteres anteriormente mencionados son variables y que no existen diferencias morfológicas discretas para considerar a *A. swallenii* como un taxón independiente. La inclusión de *A. swallenii* en la sinonimia de *A. pellitus* conlleva a que la especie posea una distribución disyunta en su distribución, lo cual puede deberse a falta de colecciones en áreas intermedias entre Pará y Paraná.

Material adicional examinado. BRASIL. **Paraná:** 8 km NE of the Paraná–Santa Catarina border at the Rio Negro, *Davidse & Ramamoorthy 11034* (F, MO); 4 km E of Guarapuava along hwy. BR-277 to Curitiba, *Davidse & Ramamoorthy 11311* (MO); Jaguariaiva, *Swallen 8664* (MO).

23. Axonopus polystachyus G. A. Black, Advancing Frontiers Pl. Sci. 5: 62, fig. 2 q, r. 1963. *Axonopus fissifolius* (Raddi) Kuhlm. var. *polystachyus* (G. A. Black) L. B. Sm. & Wassh., Fl. Il. Catarin. 1125. 1982. TIPO: Brasil. Paraná: Capão Bonito, ca. 780 m, 1 ene. 1914, *P. Dusén 14404* (holotipo, US 2236070!, US foto en SI!; isotipos, F no visto, K!, MO 878264!, MO foto en SI!, S!, SI!).

Plantas perennes, cespitosas, a veces cortamente rizomatosas; cañas erectas, de 40–100 cm de alto, 2–4 mm diám., comprimidas, simples o ramificadas en la base; entrenudos 3–6, de 7–20 cm, surcados, pajizos, estriados, glabros; nudos castaños, glabros. Vainas predominantemente basales, lateralmente comprimidas, aquilladas, formando fascículos, de 4–12 cm, glabras o esparcidamente pilosas, con pelos de base tuberculada, los márgenes membranáceos; vainas superiores hasta de 25 cm; lígulas membranáceo-ciliadas, de 0.4–0.6 mm; cuello indistinguible, glabro; láminas linear-lanceoladas a lanceoladas, de 10–40 × 1–1.7 cm, planas, estriadas, glabras a esparcidamente pilosas en ambas caras, continuándose imperceptiblemente con la vaina, ápice subagudo, los márgenes escabriúsculos, glabros a pestañosos hacia la porción basal; lámina superior reducida. Inflorescencias terminales y axilares de 10–18 × 2.5–3 cm, exertas; 1–3(4) pedúnculos emergiendo del último nudo caulinar, de 25–40 cm, angulosos, estriados, glabros; eje principal anguloso, de 20–60 × 0.5–0.7 mm; racimos 3–20, alternos, subverticilados o subdigitados, ascendentes, divergentes, los inferiores distanciados, los superiores aproximados a conjugados; raquis de los racimos triquetro, de 50–150 × 0.4–0.7 mm, glabro o con algunos pelos en los bordes hasta de 1 mm de largo, márgenes escabriúsculos; pedicelos de 0.2–0.3 mm, escabriúsculos, glabros o con algunos pelos dispersos, de 0.5–1 mm. Espiguillas largamente elipsoides, de 2.1–2.5 × 0.6–0.8 mm, de ápice agudo, pajizas, glabras o cortamente pilosas, con algunos pelos a lo largo de los nervios; gluma inferior y lema superior subiguales, 0.4–0.5 mm más largas que el antecio superior; gluma superior tan larga como la espiguilla, membranácea, 2–4-nervia, nervio medio ausente; lema inferior glumiforme, 2–4-nervia, nervio medio ausente; antecio superior elipsoide, de 1.8–2.2 × 0.6–0.7 mm, pajizo, finamente papiloso, de ápice obtuso, glabro; pálea de similar textura y ornamenta-

ción que la lema, glabra; lodículas 2, de 0.2–0.25 mm; estambres 3, anteras de 0.7–0.9 mm. Cariopsis no vista.

Hábitat y distribución. *Axonopus polystachyus* es una especie endémica del sureste (Valls et al., 2001: 138) y sur de Brasil (Paraná). Habita en campos húmedos, cerrados y en bordes de caminos en suelos modificados, a aproximadamente 800 m.s.n.m.

Nombre vulgar. "Grama-missioneira-acu" (Brasil, Smith et al., 1982: 1125 sub *Axonopus fissifolius* var. *polystachyus*).

Número cromosómico. Se ha efectuado para *Axonopus polystachyus* un recuento cromosómico de $n = 30$ (Hickenbick et al., 1975: 188 sub *A. polystachyus*).

Discusión. *Axonopus polystachyus*, miembro de la serie *Axonopus*, es morfológicamente afín a *A. compressus* por tener espiguillas de tamaño similar, antecios superiores pajizos, más cortos que la gluma superior y la lema inferior. Esta especie se distingue de *A. compressus* por tener la última un hábito estolonífero y por ser plantas gráciles, de menor porte, de 10–70(–80) cm de alto (vs. 40–100 cm en *A. polystachyus*), con láminas de 3.5–14(–25) × (0.5–)0.7–1.2 cm (vs. 10–40 × 1–1.7 cm) y espiguillas ovoides (vs. largamente elipsoides en *A. polystachyus*).

Smith et al. (1982) transfieren *Axonopus polystachyus* a una variedad de *A. fissifolius*; sin embargo el tamaño de los ejemplares de *A. polystachyus*, así como también el ancho de sus láminas (0.2–0.4[–0.5] cm en *A. fissifolius* vs. 1–1.7 cm en *A. polystachyus*), el número de racimos (dos o tres, ocasionalmente hasta seis vs. tres a 20 en *A. fissifolius* y *A. polystachyus*, respectivamente), el largo del raquis y la relación largo del antecio superior vs. largo de la gluma superior y lema inferior (de igual largo o hasta 0.3 mm más corto en *A. fissifolius* vs. 0.4–0.5 mm más corto en *A. polystachyus*) permiten distinguir a *A. polystachyus* de *A. fissifolius*.

En el ejemplar tipo de *Axonopus polystachyus* depositado en el herbario MO, *P. Dusén 14404*, se indica en la etiqueta de la cartulina como localidad de colección: "Paraná, Serra do Mar, Ypiranga locis graminosis subpaludosis, 16.I.1914".

Material adicional examinado. BRASIL. **Paraná:** Mun. Jaguariaiva, *Smith et al. 14755* (SI); Banhado–Piroquara, *Swallen 8649* (MO); Pôrto Amazonas, 5 km N, *Hatschbach 43557* (MO).

24. Axonopus pressus (Nees ex Steud.) Parodi, Notas Mus. La Plata, Bot. 3(17): 23. 1938. Basiónimo: *Paspalum pressum* Nees ex Steud., Syn. Pl. Glumac. 1: 23. 1853. TIPO: Brasil. s. loc., 1836, *F. Sellow 5638* (holotipo, B!; isotipos, B fragm. en BAA 2258!, B fragm. en LE TRIN 0512.01 no visto, B fragm. en US 2942557!, P!).

Axonopus derbyanus G. A. Black, Advancing Frontiers Pl. Sci. 5: 127. 1963. TIPO: Brasil. Mato Grosso: Campo Grande, 540–550 m, 9 (7–11) feb. 1930, *A. Chase 10836* (holotipo, US 1501229!, US 1501229 foto en SI!; isotipos, MO 3326809!, NY 346101 no visto, NY foto en SI!, US 1501230!).

Axonopus derbyanus var. *parvispicula* G. A. Black, Advancing Frontiers Pl. Sci. 5: 130. 1963. TIPO: Brasil. Goiás: Goiandira, 800–825 m, 26 mar. 1930, *A. Chase 11552* (holotipo, US 1448902!, US foto en SI!).

Plantas perennes, cespitosas, robustas, rizomatosas, con innovaciones horizontales simples o ascendentes cubiertas por numerosos catáfilos rígidos; cañas erectas de 70–150(–200) cm de alto, 3–7 mm diám., comprimidas; entrenudos 3–5, los inferiores reducidos, los superiores hasta de 18 cm, surcados, pajizos, glabros; nudos glabros, castaños a rojizos. Vainas predominantemente basales, las inferiores fasciculadas, de 4–35 cm, usualmente más largas que los entrenudos, pajizas, glabras hacia la porción inferior a densamente vilosas con pelos blanquecinos, aquilladas, los márgenes densamente pestañosos en toda su longitud o solo hacia la porción apical; lígulas membranáceo-ciliadas, de 0.5–2.5 mm, porción ciliada hasta de 1.5 mm; cuello distinguible, castaño, glabro a viloso; láminas linear-lanceoladas, de (10–) 20–45 × 0.5–2 cm, conduplicadas en la base, luego planas, verdosas, glabras en ambas caras o con la cara abaxial densamente vilosa, de base angosta continuándose imperceptiblemente con la vaina, ápice obtuso, los márgenes escabriúsculos u ocasionalmente pestañosos principalmente hacia la porción basal. Inflorescencias terminales y axilares, de 10–32 × 5–20 cm, exertas; 1–2 pedúnculos naciendo del último nudo caulinar, de 20–54 cm, cilíndricos, con un lado surcado, glabros; eje principal anguloso, de 40–140 × 0.8–1.3 mm, glabro, escabroso; racimos (10–)26–34, ascendentes, divergentes, alternos, los superiores subopuestos a subverticilados; raquis de los racimos triquetro, de (8–)13–32 cm × 0.6–0.8(–1) mm, glabro o híspidulo en los ángulos y también sobre las caras, sin pelos largos en los ángulos u ocasionalmente con 1–2 pelos hasta de 2 mm a cada lado de la base de los pedicelos; pulvínulos cortamente pilosos; pedicelos de 0.2–0.3 mm, aplanados, escabriúsculos en los ángulos, glabros a cortamente pilosos u ocasionalmente con algunos pelos largos similares a los del raquis. Espiguillas elipsoides, de 2.3–3 × 0.9–1 mm, de ápice subagudo a obtuso, pajizas o con tintes

violáceos, glabras a densamente pilosas, con pelos cortos y delicados en la base y en los espacios internervales; gluma superior y lema inferior subiguales, tan largas como el antecio superior; gluma superior tan larga como la espiguilla, membranáceo-hialina, 2–4-nervia, el nervio medio ocasionalmente presente; lema inferior glumiforme, 2–4-nervia; antecio superior elipsoide, de 2.1–2.9 × 0.7–1 mm, castaño brillante, el ápice y la base pajizos, finamente papiloso, de ápice subagudo a obtuso, glabro o con diminutos pelos blanquecinos hacia el ápice; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, de 0.2–0.3 mm, membranáceas, pajizas, conduplicadas; estambres 3, anteras de 1.4–2.5 mm, purpúreas. Cariopsis ovoide, de 1.7–1.9 × 0.6–0.8 mm, blanquecina; hilo oblongo, subbasal; embrión ca. 1/2 del tamaño de la cariopsis.

Hábitat y distribución. *Axonopus pressus* se encuentra en el centro y sur de Brasil (Goiás, Mato Grosso y Paraná), en la región oriental de Paraguay (Amambay, Caaguazú, Canindeyú, Itapúa y San Pedro) y este de Bolivia en el departamento Santa Cruz. La especie crece en cerrados, campos abiertos, en barrancos y en bordes de caminos, sobre suelos arenosos o modificados, entre los 200 y los 1300 m.s.n.m.

Nombre vulgar. "Kapí'i misione" (Paraguay, Morrone et al., 1994: 51).

Número cromosómico. Se conoce para esta especie un recuento cromosómico de $n =$ ca. 20 (Morrone et al., 1995b: 54 sub *Axonopus pressus* (Nees ex Steud.) Parodi).

Discusión. *Axonopus pressus* pertenece a la serie *Suffulti* por poseer raquis piloso, antecio superior castaño oscuro y gluma superior y lema inferior con nervio medio ausente o poco manifiesto. Esta especie es morfológicamente afín a *A. argentinus*, *A. suffultus* y *A. succulentus* G. A. Black. *Axonopus argentinus* se diferencia principalmente por presentar usualmente plantas más gráciles, con rizomas falciformes (véanse observaciones bajo *A. argentinus*). *Axonopus suffultus* se distingue de *A. pressus* por poseer vainas y láminas glaucas, violáceas (vs. pajizas, no glaucas en *A. pressus*). *Axonopus succulentus* se aparta de *A. pressus* por la presencia de aurículas foliares (vs. aurículas foliares ausentes en *A. pressus*). Para una mayor discusión sobre la variabilidad morfológica de *A. pressus* véase Cialdella et al. (2006).

Material adicional examinado. BOLIVIA. **Santa Cruz:** Prov. Velasco, Parque Nac. Noel Kempff Mercado, serranias S y NE de la pista Noel Kempff Mercado, *Mostacedo et al. 1880* (USZ). BRASIL. **Paraná:** Jaguariaiva, Parque Est. do Cerrado, *Longhi-Wagner 9468* (CTES, ICN, SI). PARAGUAY. **Amambay:** Parque Nac. Cerro Corá, *Solomon et al. 7071* (MO, PY, US). **Caaguazú:** Prope Caaguazú, *Hassler 9269a* (BAA, G). **Canindeyú:** Aguara Ñu, camino a la Comun. Tekoytra Ryapo, *Jiménez & Marin 2043* (CTES, MO). **Itapúa:** Isla Yacyretá, *Jiménez 140* (SI). **San Pedro:** Yaguareté Forest, 182 m, *Zardini & Vera 48288* (MO, SI).

25. Axonopus purpusii (Mez) Chase, J. Wash. Acad. Sci. 17: 144. 1927. Basiónimo: *Paspalum purpusii* Mez, Bot. Jahrb. Syst. 56(Beibl. 125): 10. 1921. TIPO: México. Veracruz: Zacuapán, mayo 1907, *C. A. Purpus 2450* (holotipo, B!; isotipos, B fragm. en US 2855767!, F 343969!, F foto en SI!, MO 2875301!, MO foto en SI!, US 591124!, US foto en SI!, US fragm. en SI!).

Plantas perennes, cespitosas; cañas erectas de 25–60 cm de alto, 1.4–2 mm diám., comprimidas; entrenudos 1–3, de 6–12 cm, con uno de los lados surcado, pajizos, glabros; nudos glabros, castaños. Vainas predominantemente basales, generalmente formando fascículos de 2–4 cm, glabras, aquilladas, con los márgenes membranáceos, pestañosos hacia la porción superior; vainas superiores de 6–10 cm, distantes entre sí; lígulas membranáceo-ciliadas, de 0.3–0.5 mm, cuello indistinguible, glabro; láminas lineares, de 4–20(–40) × 0.3–0.7 cm, usualmente falcadas, planas a conduplicadas, estriadas, glabras en ambas caras, de base angosta continuándose imperceptiblemente con la vaina, de ápice obtuso, ocasionalmente bífido, los márgenes membranáceos, ocasionalmente pestañosos hacia la porción basal. Inflorescencias terminales y axilares de 7–10 × 1.5–3 cm, exertas; 1–3 pedúnculos naciendo del último nudo caulinar, hasta de 30 cm, exertos o subincluidos en las vainas, filiformes, glabros; eje principal anguloso, de 8–24 × 0.5–0.8 mm; racimos 2–5, ascendentes, divergentes, alternos, los superiores aproximados a conjugados; raquis de los racimos triquetro, de 4–10(–12) × 0.4–0.6 cm, glabro, con los márgenes escabriúsculos; pedicelos de 0.2–0.3 mm, glabros, escabriúsculos, de ápice oblicuo. Espiguillas elipsoides de 1.8–2.3(–2.5) × 0.6–0.8 mm, insertas oblícuamente en los pedicelos, híspidas, con pelos dorados a castaño brillantes en la base, a lo largo de los nervios y en el ápice, ápice agudo, pajizas o con tintes violáceos; gluma inferior y lema superior subiguales, tan largas como en antecio superior o ligeramente mayores; gluma superior tan larga como la espiguilla, membranácea, 2(–4)-nervia, el nervio medio ausente; lema inferior glumiforme, 2-nervia, el nervio medio ausente; antecio superior elipsoide, de

1.7–2.2 × 0.6–0.7 mm, pajizo, finamente papiloso, de ápice agudo, con un mechón de pelos blanquecinos tiesos hacia el ápice; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, ca. 0.2 mm; estambres 3, anteras de 1–1.3 mm. Cariopsis no vista.

Hábitat y distribución. *Axonopus purpusii* se halla desde México y Centroamérica (Black, 1963: 40, 41), extendiéndose en Sudamérica hasta el este de Bolivia, donde crece en el departamento Santa Cruz y la región nordoriental de Paraguay, en los departamentos de Amambay y Concepción. Esta especie es frecuente en las sabanas y llanos del norte de Sudamérica, en ambientes abiertos y soleados desde el nivel del mar hasta los 1000 m.s.n.m. *Axonopus purpusii* es utilizada como forrajera en áreas inundables del norte de Sudamérica, en particular durante la estación de lluvias (Black, 1963).

Números cromosómicos. Existen para esta especie recuentos cromosómicos de $n = 10$ (Hickenbick et al., 1975: 188 sub *Axonopus purpusii* (Mez) Chase) y $2n = 20$ (Pohl & Davidse, 1971: 299 sub *A. purpusii*).

Discusión. *Axonopus purpusii* pertenece a la serie *Axonopus* por tener antecio superior claro, pajizo, gluma superior y lema inferior con nervio medio ausente y ápice de las laminas agudo a obtuso, no setáceo. Esta especie es morfológicamente afín a *A. fissifolius*, distinguiéndose de esta última por tener las espiguillas insertas oblícuamente sobre los pedicelos (vs. no insertas oblícuamente en *A. fissifolius*), híspidas, con un denso mechón de pelos de color dorado a castaño brillante (vs. espiguillas glabras, ocasionalmente cortamente pilosas, con pelos blanquecinos en *A. fissifolius*).

Mez (1921) al describir *Axonopus purpusii* no cita la inserción oblícua de la espiguilla como característica de la especie; no obstante, esta característica, sumada a la pilosidad de la espiguilla, el hábito cespitoso y la presencia de vainas basales fasciculadas distinguen a esta especie de las otras de la serie *Axonopus*.

Material adicional examinado. BOLIVIA. **Santa Cruz:** Ñúflo de Chávez, Ea. La Pachanga, 5 km S of Concepción, *Killeen 2253* (CTES, MO, SI, USZ). PARAGUAY. **Amambay:** In regione cursus superioris fluminis Apa, *Hassler 8248* (G, LIL, MO); Parque Nac. Cerro Corá, Remonta Cué, *Morrone & Pensiero 559* (MO, SI). **Concepción:** Zwischen Río Apa und Río Aquidabán, Caballero Cué, *Fiebrig 4910* (G, SI).

26. Axonopus rosengurttii G. A. Black, Advancing Frontiers Pl. Sci. 5: 64. 1963. TIPO: Uruguay. Paysandú: Isla Queguay en el Río Uruguay, de matas cultivadas en Monzón-Heber (Soriano), ene. 1944, *B. Rosengurtt B 3818-1/2* (holotipo, US 1865690!, US foto en SI!; isotipos, K no visto, US fragm. en SI!).

Plantas perennes, estoloníferas, en ocasiones cespitosas; cañas erectas a decumbentes, de 20–50 cm de alto, 1.9–3 mm diám., comprimidas; entrenudos 1–4, de 3–11 cm, estriados, pajizos, glabros; nudos glabrescentes a pilosos, castaños. Vainas predominantemente basales o distribuidas a lo largo de la caña, de 2–8 cm, glabras, aquilladas, los márgenes membranáceos; vainas superiores de 7–15 cm; lígulas membranáceo-ciliadas, de 0.7–0.8 mm, cuello distinguible, algo piloso en los márgenes; láminas linear a linear-lanceoladas, de 5–15 × 0.5–1 cm, planas, glabras en ambas caras, de base angosta y ápice subagudo a obtuso, los márgenes escabriúsculos. Inflorescencias terminales y axilares de 6–11 × 0.8–2 cm, exertas; pedúnculos 2–4(5), hasta de 22 cm, filiformes, glabros, con un lado surcado; eje principal de 0–1.5 cm, anguloso, glabro; racimos 2(3), ascendentes, divergentes, aproximados a subconjugados; raquis de los racimos triquetro, de 40–100 × 0.6–0.8 mm, glabro, bordes escabriúsculos; pedicelos de 0.2–0.3 mm, glabros, escabriúsculos en los márgenes. Espiguillas elipsoides, de (2.7–)3.4–4 × 1–1.2 mm, de ápice agudo a subagudo, pajizas a verdosas, glabras o con unos pocos pelos suaves en la base, gluma superior y lema inferior subiguales, 0.6–0.8 mm mayores que el antecio superior; gluma superior tan larga como la espiguilla, membranácea, (2–)4-nervia, con el nervio medio ausente o cuando presente delicado; lema inferior glumiforme, (2–)4-nervia, el nervio medio ausente; antecio superior elipsoide, de 2.5–3.2 × 0.9–1.1 mm, pajizo, finamente papiloso, de ápice agudo, con un mechón de pelos blanquecinos hacia el ápice; pálea similar en textura y ornamentación a la lema, glabra; lodículas 2, de 0.3–0.4 mm; estambres 3, anteras de 1.2–1.3 mm. Cariopsis no vista.

Hábitat y distribución. *Axonopus rosengurttii* es una especie presente en Argentina (Buenos Aires y Distrito Federal) y Uruguay (Paysandú) sobre la ribera del Río Uruguay y del Río de la Plata. Habita en áreas húmedas formando céspedes desde el nivel del mar hasta 100 m.s.n.m.

Discusión. *Axonopus rosengurttii* pertenece a la serie *Axonopus* por tener, al igual que *A. purpusii*, antecio superior claro, pajizo, gluma superior y lema inferior con nervio medio ausente y ápice de las láminas agudo a obtuso, no setáceo. Esta especie es morfológicamente afín a *A. obtusifolius* por el tipo de hábito estolonífero, inflorescencias con pocos racimos

y espiguillas grandes, distinguiéndose esta última especie por tener los racimos distanciados sobre el eje principal. *Axonopus compressus* también está relacionada con *A. rosengurttii*, pero ésta última presenta generalmente dos racimos y espiguillas de mayor tamaño, de 3.4–4 mm de largo (vs. 2–2.6 mm en *A. compressus*).

Material adicional examinado. ARGENTINA. **Buenos Aires:** San Isidro, ribera del Río de la Plata, *Parodi 15282* (BAA). **Distrito Federal:** Facultad de Agronomía, *Parodi 151* (BAA).

27. Axonopus scoparius (Flüggé) Kuhlm., Relat. Comiss. Linhas Telegr. Estratég. Matto Grosso Amazonas 67(11): 45. 1922. Basiónimo: *Paspalum scoparium* Flüggé, Gram. Monogr., Paspalum 124. 1810. TIPO: Venezuela. s. loc., s.d., *F. W. H. A. von Humboldt & A. J. A. Bonpland s.n.* (holotipo, P-Bonpl.!; isotipos, B-W y P fragm. en US 80014!, P fragm. en SI!).

Paspalum tripinnatum Mez, Repert. Spec. Nov. Regni Veg. 15: 64. 1917. TIPO: Bolivia. La Paz: "Yungas Austr., Sirupaya prope Yanacachi", s.d., *O. Buchtien 410* (holotipo, B!; isotipos, M no visto, M fragm. en US 80054!).

Plantas perennes, robustas, cespitosas a estoloníferas, arraigadas en los nudos inferiores; cañas erectas de 70–200 cm de alto, 4–13 mm diám., cilíndricas o comprimidas; entrenudos 3–8, de 5–22 cm, estriados, levemente surcados, pajizos, glabros; nudos glabros o pilosos, pelos cortos, blanquecinos y adpresos. Vainas predominantemente basales, generalmente formando fascículos, de 10–35 cm, glabras o algo pilosas hacia la región lígular, aquilladas, estriadas, los márgenes membranáceos, glabros a pestañosos hacia la porción superior; lígulas membranáceo-ciliadas, de 0.8–2 mm, cuello distinguible, generalmente piloso, con pelos hasta de 2.5 mm, castaño; láminas lanceoladas, de 15–50 × 0.7–4 cm, planas, con el nervio medio conspicuo, glabras a esparcidamente pilosas, con pelos de base tuberculada, base angosta y ápice agudo a subagudo, los márgenes escabriúsculos. Inflorescencias terminales o axilares de 12–35 × (5–)8–20 cm, exertas; 1–3 pedúnculos naciendo del último nudo caulinar, de 15–48 cm × 1–1.8 mm, cilíndricos a angulosos, surcados, pajizos, glabros, los márgenes escabriúsculos; eje principal anguloso, de 8–30 cm × 0.8–1.2 mm, glabro a glabrescente, los márgenes escabriúsculos; racimos 10–100 o más, ascendentes, divergentes, alternos a subopuestos o verticilados, los inferiores usualmente ramificados; raquis de los racimos triquetro, de 100–250 × 0.3–0.7 mm, glabro a glabrescente; pulvínulos cortamente pilosos; pedicelos de 0.4–0.6(–3) mm, glabros a glabrescentes, los márgenes escabriúsculos. Espiguillas elipsoides, de 2.3–2.8 × 0.7–0.9 mm, de ápice agudo, pajizas o con tintes violáceos, glabrescentes a esparcidamente pilosas entre los nervios; gluma superior y lema inferior subiguales, 0–0.3 mm más largas que el antecio superior; gluma superior tan larga como la espiguilla, membranácea, 5-nervia, los nervios prominentes, en ocasiones el nervio medio ausente; lema inferior glumiforme, (4)5-nervia; antecio superior anchamente elipsoide, de 1.9–2.4 × 0.7–0.9 mm, pajizo, finamente papiloso, de ápice subagudo, glabro o con unos pocos pelos cortos blanquecinos en el ápice; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, de 0.2–0.4 mm; estambres 3, anteras de 1.3–1.5 mm, purpúreas. Cariopsis no vista.

Hábitat y distribución. Axonopus scoparius se encuentra desde Mesoamérica (Black, 1963: 113), hasta Colombia (Black, 1963: 113), Venezuela, Perú (Black, 1963: 114), Brasil (Black, 1963: 114) y Bolivia, en los departamentos de Cochabamba, La Paz y Santa Cruz. La especie se halla en bordes de caminos, campos abiertos, pastizales y bordes de bosques, entre 200 y 2100 m.s.n.m. *Axonopus scoparius* tiene importancia económica, siendo cultivada como forraje en Centroamérica y en la región Andina de sudamérica desde Colombia hasta Bolivia.

Nombres vulgares. "Sara-sara", "Cachi", "Gramillote" (Bolivia, Black, 1963: 114); "Capin imperial", "capim touceira", "capin colombiano", "capin branco" (Brasil, Black, 1963: 114).

Números cromosómicos. Se han llevado a cabo para *Axonopus scoparius* recuentos cromosómicos de $n = 30$ (Morrone et al., 2006: 648 sub *A. scoparius* (Flüggé) Kuhlm.); $2n = 20$ (Pohl & Davidse, 1971: 299 sub *A scoparius*).

Discusión. Axonopus scoparius pertenece a la serie *Barbigeri* por incluir plantas robustas, inflorescencias con numerosos racimos, gluma superior y lema inferior con nervios manifiestos y antecio superior claro. Esta especie es morfológicamente afín a *A. iridifolius* (véanse observaciones bajo esta especie).

Axonopus scoparius posee una marcada variabilidad en relación al hábito y la coloración de las espiguillas, reconociéndose dos formas, una de ellas llamada "pasto micay" que incluye plantas de porte bajo y otra robusta, conocida como "pasto imperial" o "gramalote" (Black, 1963: 18). También es variable el número de racimos, hallándose ejemplares con

pocos racimos y otros con más de 100 (Salariato, observ. pers.).

Mez (1917) al describir *Paspalum tripinnatum* cita el ejemplar *Buchtien 1410* como tipo de la especie. El ejemplar tipo depositado en US (80054) consiste de un fragmento proveniente del herbario M y en la cartulina con letra de A. Chase se señala que existe un error en el número de colección 1410 por 410.

Material adicional examinado. BOLIVIA. **Cochabamba:** just below Incachaca (off Cochabamba–Charapa rd.), *Wood 9623* (LPB). **La Paz:** Prov. Nor Yungas, 15 km from Yolosa on rd. to La Paz, *Renvoize 4775* (K, LPB, MO). **Santa Cruz:** Prov. Florida, Parque Nac. Amboró, Río San Rafael, 10 km al NE de Mairana, *Vargas et al. 2035* (MO, USZ).

28. Axonopus siccus (Nees) Kuhlm., Relat. Comiss. Linhas Telegr. Estratég. Matto Grosso Amazonas 67(11): 87. 1922. Basiónimo: *Paspalum siccum* Nees, Fl. Bras. Enum. Pl. 2(1): 28. 1829, como "*Paspalus siccus*". TIPO: Brasil. Minas Gerais: "in districtu Adamantum", s.d., *K. F. P. von Martius s.n.* (holotipo, M no visto, M foto en SI!; isotipos, M fragm. en LE TRIN 0533.01!, M fragm. en SI!, M fragm. en US 80020!).

Paspalum barbatum Nees ex Trin., Sp. Gram. 1: tab. 98. 1827, nom. illeg. superfl., non *Paspalum barbatum* (Trin.) Schult., 1827. Replacement name: *Paspalum barbigerum* Kunth, Révis. Gramin. 1: 24. 1829. *Axonopus barbiger* (Kunth) Hitchc., Contr. U.S. Natl. Herb. 24(8): 433. 1927, as "*barbigerus*". TIPO: Brasil. "Brasilia meridionalis", s.d., *F. Sellow s.n.* [de Schlechtendal, 1827] (holotipo, LE 0419.04!, LE foto en SI!; isotipos, LE fragm. en US 2942150!, LE fragm. en SI!).

Paspalum eminens Nees, Fl. Bras. Enum. Pl. 2(1): 30. 1829, syn. nov. *Axonopus eminens* (Nees) G. A. Black, Advancing Frontiers Pl. Sci. 5: 92. 1963. TIPO: Brasil. s. loc., s.d., *K. F. P. von Martius s.n.* (holotipo, M!; isotipos, LE TRIN 0449.01 no visto, M fragm. en SI!, M fragm. en US 2854685!).

Paspalum barbatum var. *laxius* Döll, Fl. Bras. 2(2): 108. 1877. *Axonopus siccus* (Nees) Kuhlm. var. *laxior* (Döll) G. A. Black, Advancing Frontiers Pl. Sci. 5: 99. 1963. TIPO: Brasil. s. loc., s.d., *L. Riedel 891* (holotipo, LE no visto; isotipos, B fragm. en US 2854147!, B fragm. en US 2854148!, BM fragm. en US 2854148!, LE fragm. en US 2854148!).

Paspalum barbatum var. *scabrum* Pilg., Bot. Jahrb. Syst 30(1): 130. 1901. *Axonopus siccus* var. *scaber* (Pilg.) G. A. Black, Advancing Frontiers Pl. Sci. 5: 99, fig. 3o–p. 1963. TIPO: Brasil. Mato Grosso: Cuiabá, abr. 1899, *H. Meyer 521* (holotipo, B!; isotipos, B fragm. en SI!, B fragm. en US 2942151!).

Paspalum ulei Hack., Oesterr. Bot. Z. 51: 240. 1901. *Axonopus ulei* (Hack.) Dedecca, Bragantia 15: 276. 1956. TIPO: Brasil. Santa Catarina: s. loc., mar. 1894, *E. Ule 3526* (lectotipo, aquí designado, W!; duplicado, US 80048!, US foto y fragm. en SI!).

Axonopus barbiger (Kunth) Hitchc. var. *venturii* G. A. Black, Advancing Frontiers Pl. Sci. 5: 97, fig. 3k. 1963, as "*Axonopus barbigerus* var. *venturi*". TIPO: Argentina. Tucumán: Dpto. Burruyaco, Cerro del Campo, 2000 m, 29 mayo 1930, *S. Venturi 10242* (holotipo, US 1447338!, US foto en SI!; isotipo, IAN no visto).

Axonopus eminens (Nees) G. A. Black var. *bolivianus* G. A. Black, Advancing Frontiers Pl. Sci. 5: 93, f. 31. 1963, syn nov. TIPO: Bolivia. Beni: near Reyes, 300 m, abr. 1947, *H. C. Cutler 9088* (holotipo, US 2013341!, US foto en SI!; isotipo, US fragm. en SI!).

Axonopus rojasii G. A. Black, Advancing Frontiers Pl. Sci. 5: 100. 1963. TIPO: Paraguay. Cordillera: Piribebuy, Salto Piraretá, mar. 1942, *T. Rojas 9515* (holotipo, US 2012986!; isotipo, US fragm. en SI!).

Axonopus pilosus G. A. Black, Advancing Frontiers Pl. Sci. 5: 100, tab. 6. 1963. TIPO: Bolivia. "Tucumilla bei Tarija", 2600 m, 30 mar. 1904, *K. Fiebrig 2782* (holotipo, GH p.p. [pl. de la derecha]!, GH foto en US 2941907!; isotipos, GH fragm. en SI!, GH fragm. en US 2941907!).

Axonopus perlongus G. A. Black, Advancing Frontiers Pl. Sci. 5: 89. 1963. TIPO: Brasil. Mato Grosso: Tres Lagôas, 300–325 m, 4–5 feb. 1930, *A. Chase 10730* (holotipo, US 1501001!; isotipo, US 1501001 fragm. en SI!).

Axonopus malmei G. A. Black, Advancing Frontiers Pl. Sci. 5: 101, fig. 7. 1963. TIPO: Brasil. Rio Grande do Sul: Porto Alegre, Morro da Policia, 21 feb. 1902, *G. O. A. Malme 1402* (holotipo, GH!, GH foto en US 2941911!; isotipos, GH fragm. en SI!, GH fragm. en US 2941911!).

Plantas perennes, cespitosas, de rizomas cortos; cañas de 0.5–2.3 m de alto, 3–7 mm diám., cilíndricas a comprimidas; entrenudos 3 a numerosos, de 6–50 cm × 2–8 mm, finamente estriados, glabros a glabrescentes; nudos glabros a híspidos, castaños a púrpuras. Vainas de 6–40 cm, glabras o esparcidamente pilosas, los márgenes membranáceos, esparcidos a densamente pilosos en toda su longitud o solamente hacia la porción apical; lígulas membranáceo-ciliadas, de 0.3–2.6 mm, de base cortamente membranácea, luego largamente pestañosa, con pelos hasta de 0.7 mm, blanquecinos; cuello distinguible, glabro, castaño; láminas filiformes a lineares, de 7–90 × 0.1–1.2 cm, conduplicadas a planas en la porción superior, rígidas, glabras a esparcidamente pilosas, lisas o escabrosas, de base angostada, en ocasiones formando un pseudopecíolo, el ápice largamente agudo, pungente, gradualmente agudo, los márgenes membranáceos, lisos o escabriúsculos; las inferiores usualmente filiformes; las superiores más anchas, con la porción media plana y los bordes planos, involutos a fuertemente plegados. Inflorescencias terminales y axilares, de 10–60 × 3–10 cm, exertas; 1(2) pedúnculos, de 15–60 cm, cilíndricos, finamente estriados, glabros; eje principal de 6–30 cm, anguloso, con los márgenes lisos o escabriúsculos; racimos (3–)7–60, ascendentes, divergentes, alternos a subopuestos o subverticilados, los superiores aproximados; raquis de los racimos

triquetro, de 6–20 cm × 0.4–0.7 mm, glabro, con los márgenes escabriúsculos, glabros a esparcidamente pubescentes; pulvínulos pilosos; pedicelos triquetros, de 0.2–0.8 mm, glabros o con unos pocos pelos cortos, escabriúsculos. Espiguillas elipsoides, (1.6–) 1.8–3(–3.6) × 0.6–1 mm, de ápice subagudo, pajizas a púrpuras, glabras a esparcidamente pilosas entre los nervios y en la porción basal; gluma superior y lema inferior subiguales, del mismo tamaño que el antecio superior; gluma superior tan larga como la espiguilla, membranácea, 5–7-nervia, con los nervios prominentes; lema inferior glumiforme, 5–7-nervia; antecio superior elipsoide, 1.6–2.9 × 0.6–0.9 mm, pajizo, finamente papiloso, de ápice agudo a subagudo, glabro o con unos pocos pelos blanquecinos hacia el ápice; pálea superior de similar textura y ornamentación que la lema, glabra; lodículas 2, de 0.2–0.4 mm, cuneadas; estambres 3, anteras de 1.2–2.1 mm, púrpuras. Cariopsis elipsoide, de 2 × 0.6 mm, pálida; hilo punctiforme, subbasal; embrión 1/2 o un poco menos del largo de la cariopsis.

Hábitat y distribución. *Axonopus siccus* posee una amplia distribución desde el norte de Sudamérica hasta Brasil, Bolivia, Paraguay, Uruguay y norte de Argentina. Crece en campos secos o bajos, en suelos arenoso-arcillosos, en arbustales, en bordes de bosques y en regiones montañosas sobre suelos rocosos hasta los 2800 m.s.n.m.

Nombre vulgar. "Capim cabeludo" (Brasil, Smith et al., 1982: 1130).

Número cromosómico. Hasta el momento se ha completado un recuento para esta especie de $n = 10$ (Morrone et al., 1995b: 54 sub *Axonopus siccus* (Nees) Kuhlm.).

Discusión. *Axonopus siccus* es una especie polimorfa, con una marcada variación en los caracteres morfológicos, en particular en la pilosidad de las vainas, hojas y espiguillas, tamaño de la planta y espiguillas y forma de las hojas, razón por la cual se han descriptos numerosos taxones bajo esta especie. Con respecto a la forma de las láminas, esta puede variar de filiformes, no superando los 0.3 cm de ancho, o ejemplares donde alternan láminas filiformes con láminas planas hasta de 0.8 cm de ancho. En relación a la longitud de las espiguillas podemos encontrar ejemplares con espiguillas que van desde 1.8 a 3 mm a otros que llegan a los 3.6 mm de largo. Otro carácter altamente variable es la pilosidad de las vainas y láminas, hallándose ejemplares glabros o pilosos, con diferente grado de densidad de la pilosidad.

El análisis del ejemplar tipo de *Axonopus pilosus*, depositado en el herbario GH, permitió confirmar las observaciones de Foster (1966), quién señala que la cartulina posee mezcla de dos plantas: la planta de la derecha corresponde a *A. pilosus* y la planta de la izquierda corresponde a un ejemplar del género *Trachypogon* Nees. Cabe destacar que los fragmentos conservados en SI y US corresponden al ejemplar de la derecha, conservado en la cartulina de GH, y que es *A. pilosus*.

Axonopus eminens ha sido distinguido de *A. siccus* por tener principalmente láminas angostas, pseudopecioladas y aplanadas hacia la porción superior. El análisis de abundante material de herbario permitió observar que existe una gradación en el ancho de la lámina; incluso se pudo observar en un mismo ejemplar la presencia de hojas planas y filiformes. Por lo anteriormente expuesto se considera que no existen diferencias significativas para mantener a *A. eminens* como una entidad independiente y se la incluye bajo la sinonimia de *A. siccus*.

Hackel (1901) al describir *Paspalum ulei* cita dos sintipos: *Ule 3526* y *1950*, de los cuales se ha seleccionado el ejemplar *Ule 3526* como lectotipo de la especie por ajustarse al protólogo de la especie.

Material adicional examinado. ARGENTINA. **Corrientes:** Dpto. Empedrado, Ea. Tres Marías, cercano al Río Parana, *Schinini 34411* (CTES, SI). **Jujuy:** Dpto. Palpalá, Sierra de Zapla, Mina 9 de Octubre, *Zuloaga et al. 5858* (CTES, MO, SI). **Misiones:** Apóstoles, Escuela Agrotécn. Pascual Gentilini, Cerro Ceferino, *Zuloaga et al. 4923* (CTES, MO, SI). **Salta:** Dpto. Santa Victoria, Ruta Prov. 19, 10 km de los Toldos camino a Lipeo, *Morrone et al. 3776* (CTES, MO, SI). **Tucumán:** Tafí, *Venturi 10032* (MO). BOLIVIA. **Beni:** Prov. Ballivián, Est. Biol. Beni, 40 km al E de San Borja, *Killeen 2819* (LPB, MO). **Chuquisaca:** Prov. Sucre, Sucre, *Wood 7864* (LPB, MO). **Cochabamba:** Campero, *Antezana 1251* (MO). **La Paz:** Prov. Nor Yungas, arriba de Coroico, *Beck 17469* (LPB, USZ). **Santa Cruz:** Prov. Velasco, Parque Nac. Noel Kempff Mercado, *Killeen et al. 6040* (CTES, LPB, MO, SI, USZ). **Tarija:** Prov. Arce, entre Padcaya y Cañas, subiendo de la Ea. Cabildo hacia el Cerro Cabildo, *Beck & Liberman 16256* (LPB). BRASIL. **Paraná:** Mun. Alm. Tamandaré, Rod. Dos Minerios, Rio Barigui, *Hatschbach 44605* (MBM, MO). **Rio Grande do Sul:** Colonia Sta. Flora, *Costa Sacco 393* (F). **Santa Catarina:** 5 km N of Lajes along hwy. BR-116, *Davidse & Ramamoorthy 11118* (MO). PARAGUAY. **Amambay:** In altaplanitie et declivibus Sierra de Amambay, *Hassler 10171* (G, LIL, US). **Caaguazú:** Km 111, San José, *Rosengurtt B-5871* (BAA, LIL). **Central:** San Antonio, *Rojas 10366* (BAA, US). **Concepción:** Ea. Arrecife, *Zardini & Espinoza 53733* (MO, SI). **Cordillera:** Ybytu Silla, *Zardini et al. 26188* (MO, SI). **Guairá:** Colonia Independencia, Cerro Pelado, *Rojas 4822* (BAA). **Itapuá:** San Pedro del Paraná, *Jiménez 13509* (BAA). **Misiones:** San Ignacio, *Rosengurtt B-5780* (LIL). **Paraguarí:** Cerro Yaguarón, *Balansa 96* (G). **San Pedro:** La Manina, *Pedersen 11051* (CTES, F, SI). URUGUAY. **Rivera:** Batovi, *Pedersen 15694*

(CTES, F, MO). **Tacuarembó:** Tacuarembó, *Pinto s.n.* (BAA).

29. Axonopus succulentus G. A. Black, Advancing Frontiers Pl. Sci. 5: 134. 1963. TIPO: Paraguay. Paraguarí: Ybytymí Cordillerita, feb. 1933, *T. Rojas 6176* (holotipo, US 2012951!, US foto en SI!; isotipo, BAA!).

Plantas perennes, robustas, rizomatosas, con vástagos cubiertos por catáfilos rígidos; cañas erectas, de 60–120 cm de alto, levemente cilíndricas; entrenudos 3–6, longitudinalmente estriados, glabros; nudos glabros a pubérulos, castaños. Vainas predominantemente basales, de 8–30 cm, generalmente menores que los entrenudos, glabras, aquilladas, longitudinalmente estriadas, pajizas, con los márgenes membranáceos, lisos; aurículas presentes; lígulas membranáceo-ciliadas, de 1–1.5 mm, con la cara abaxial pubescente, la restante glabra, pajizas; cuello distinguible, glabro; aurículas presentes; láminas linear-lanceoladas, de 30–52 × 1–2 cm, plegadas en la base, luego planas, longitudinalmente estriadas, glabras en ambas caras, de base redondeada continua con la vaina, el ápice obtuso, los márgenes membranáceos, rara vez escabriúsculos. Inflorescencias terminales y axilares de 15–25 × (8–)12–20 cm, exertas; pedúnculos 2–3, de 30–45 cm, cilíndricos, con surco lateral conspicuo, longitudinalmente estriado, glabro; eje principal de 2–5 cm, anguloso, surcado, escabriúsculo en los márgenes; racimos 15–18(–25), ascendentes, divergentes, alternos, los superiores subopuestos a subverticilados; raquis de los racimos triquetro, de (8–)12–20 cm × 0.5–0.8 mm, glabro, los márgenes hispídulos, con 3–4 pelos de 1–1.2 mm a cada lado de la base de cada pedicelo; pulvínulos cortamente pilosos; pedicelos aplanados, de 0.3–0.5 mm, glabros o cortamente pilosos. Espiguillas elipsoides, de 2.1–2.4 × 0.7–1 mm, de ápice subagudo a obtuso, ocreáceas, glabrescentes a esparcidamente pilosas, con pelos delicados, distribuidos en los espacios internervales; gluma superior y lema inferior subiguales, tan largas como el antecio superior; gluma superior tan larga como la espiguilla, membranácea, delicada, 2(3)-nervia; lema inferior glumiforme, 2(3)-nervia; antecio superior elipsoide, de 2–2.2 × 0.8 mm, castaño, brillante, pajizo hacia el ápice y la base, finamente papilosa en el dorso, de ápice subagudo, glabro; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, conduplicadas; estambres 3, anteras ca. 1.5 mm. Cariopsis no vista.

Hábitat y distribución. *Axonopus succulentus* es una especie endémica de la región oriental del Paraguay, en el departamento Paraguarí, donde crece en campos.

Nombre vulgar. "Kapí i kyra" (Paraguay, Morrone et al., 1994: 60).

Discusión. *Axonopus succulentus* es un miembro de la serie *Suffulti* por tener antecio superior castaño, raquis usualmente piloso y gluma superior y lema inferior usualmente ausente. Dentro de esta serie, *A. succulentus* conocida únicamente por la colección tipo, se diferencia de *A. pressus* por tener aurículas conspicuas (vs. ausentes en *A. pressus*).

30. Axonopus suffultus (J. C. Mikan ex Trin.) Parodi, Notas Mus. La Plata, Bot. 3(17): 23. 1938. Basiónimo: *Paspalum suffultum* J. C. Mikan ex Trin., Neue Entdeck. Pflanzenk. 2: 46. 1821. *Panicum suffultum* (J. C. Mikan ex Trin.) Kuntze, Revis. Gen. Pl. 3(3): 364. 1898. *Axonopus scoparius* var. *suffultus* (J. C. Mikan ex Trin.) Herter, Anales Mus. Hist. Nat. Montevideo 3(1): 49. 1929. *Axonopus suffultus* (J. C. Mikan ex Trin.) Henrard, Blumea 4(3): 510. 1941, nom. illeg. TIPO: Brasil. s. loc., s.d., *J. C. Mikan s.n.* (holotipo, LE TRIN 0537.07!, LE foto en SI!; isotipos, LE fragm. en SI!, LE fragm. en US 80029!).

Panicum hagenbeckianum Kuntze, Revis. Gen. Pl. 3(3) 361. 1898. *Anthaenantia hagenbeckiana* (Kuntze) K. Schum., Just's Bot. Jahresber. 261: 329. 1900. *Axonopus hagenbeckianus* (Kuntze) Parodi, Notas Mus. La Plata, Bot. 3(17): 21. 1938. TIPO: Argentina/Bolivia. Gran Chaco, s.d., *C. F. Hagenbeck s.n.* (lectotipo, aquí designado, US 80689! [fragm. ex B]; duplicado, BAA 316! [fragm. ex B]).

Paspalum iridaceum Mez, Bot. Jahrb. Syst. 56(Beibl. 125): 10. 1921. *Axonopus iridaceus* (Mez) Hitchc. & Chase ex Rojas, Revista Jard. Bot. Mus. Hist. Nat. Paraguay 2: 160. 1930. *Axonopus iridaceus* (Mez) Henrard, Blumea 4(3): 510. 1941, nom. illeg. superfl. *Axonopus hagenbeckianus* (Kuntze) Parodi var. *iridaceus* (Mez) G. A. Black, Advancing Frontiers Pl. Sci. 5: 140. 1963. TIPO: Paraguay. Amambay: Sierra de Amambay, oct. 1912, *E. Hassler 11413* (holotipo, B!; isotipos, B fragm. en BAA 317!, B fragm. en SI!, B fragm. en US 2855289!, G!, MO 2101066!, MO foto en SI!, US 725414!).

Axonopus chloridiformis Herter, Revista Sudamer. Bot. 10: 130. 1956, nom. nud.

Plantas perennes, densamente cespitosas, con rizomas de entrenudos cortos y macollos dísticos de aspecto iridaceo; cañas erectas, robustas, de 50–150 × 0.3–0.6 cm diám., levemente comprimidas; entrenudos 2–4, de 10–30 cm, con uno de los lados surcado, pajizos, glabros; nudos generalmente glabros, a veces con algunos pelos a la altura del cuello, castaños. Vainas predominantemente basales, fasci-

culadas, de aspecto iridáceo, de 5–25 cm, menores que los entrenudos, glaucas o no, usualmente con tintes violáceos, conduplicadas, aquilladas, rígidas, los márgenes membranáceos, glabros; lígulas membranáceo-ciliadas, de 0.4–0.6 mm, castañas; cuello indistinguible, glabro; láminas lineares, de 18–55 × 0.4–1.3 cm, conduplicadas en la base, luego planas, glabras, glaucas, rígidas, la base continuándose imperceptiblemente con la vaina, de ápice obtuso, en ocasiones bífido, los márgenes lisos, en ocasiones escabriúsculos, glabros o esparcidamente pilosos hacia la porción inferior. Inflorescencias terminales y axilares de 10–28 × 3–12 cm, exertas; 1–2 pedúnculos naciendo del último nudo caulinar, de 15–60 cm, cilíndricos, con surco lateral, longitudinalmente estriado, glabro; eje principal anguloso, de 25–120 × 0.8–1 mm, glabro, escabriúsculo; racimos 8–23(–40), ascendentes, divergentes, alternos, subopuestos a verticilados, los superiores aproximados; raquis de los racimos triquetro, de (4–)11–22 cm × 0.4–0.6 mm, con (2)3–4(–6) pelos blanquecinos, de 1–2 mm, sobre los ángulos a cada lado de la base de los pedicelos, los márgenes escabriúsculos; pulvínulos pubérulos; pedicelos triquetros, de 0.2–0.5 mm, escabriúsculos, pudiendo tener algunos pelos similares a los del raquis. Espiguillas elipsoides, de 1.8–2.2(–2.5) × 0.6–1 mm, glabras, de ápice agudo, castaño claras, glabras; gluma inferior y lema superior subiguales, del mismo tamaño que el antecio superior o superándolo hasta 0.2 mm; gluma superior 1.9–2.5 mm, tan larga como la espiguilla o ligeramente mayor, hialina, delicada, 2(3)-nervia, el nervio medio ausente o en ocasiones presente; lema inferior glumiforme, 2-nervia; antecio superior elipsoide, de 1.8–2.2(–2.4) × 0.6–0.9 mm, castaño brillante, pajizo en el ápice y la base, finamente papiloso, el ápice subagudo a obtuso, glabro; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, ca. 0.2 mm, conduplicadas; estambres 3, anteras de 1–1.2 mm, purpúreas. Cariopsis elipsoide, de 1.4–1.6 × 0.6–0.7 mm; hilo oblongo, subbasal; embrión 1/2 del largo de la cariopsis.

Hábitat y distribución. *Axonopus suffultus* se distribuye en el sur de Brasil (en los estados de Paraná, Rio Grando do Sul y Santa Catarina), Uruguay (Cerro Largo, Florida, Paysandú, Rocha, San José y Tacuarembó), Paraguay (Alto Paraná, Amambay, Caaguazú, Canindeyú, Central, Cordillera, Guairá, Itapúa, Misiones, Paraguarí y San Pedro) y noreste y centro de la Argentina (Buenos Aires, Chaco, Córdoba, Corrientes, Entre Ríos, Formosa, Misiones y Santa Fe). Crece en suelos bajos, arenoso-arcillosos, o bien en suelos pedregosos, secos, en campos abiertos donde es frecuente en áreas sujetas a fuegos periódicos, siendo común hallar en las bases de las plantas restos de vainas quemadas, desde el nivel del mar hasta los 1700 m.s.n.m.

Nombre vulgar. "Palha-dura" (Brasil, Smith et al., 1982: 1133).

Números cromosómicos. Hasta el presente se han citado para *Axonopus suffultus* recuentos coincidentes de $n = 10$ (Hunziker et al., 1998: 31 sub *A. suffultus* (J. C. Mikan ex Trin.) Parodi) y $2n = 20$ (Saura, 1948: 54, sub *A. iridaceus* (Mez) Hitchc. & Chase ex Rojas; Núñez, 1952: 239 sub *A. iridaceus*).

Discusión. *Axonopus suffultus* se caracteriza por su hábito cespitoso, con rizomas de entrenudos cortos, formando matas densas, con cañas erectas, con las vainas basales marcadamente fasciculadas, siendo estas usualmente glaucas y violáceas. Es una especie morfológicamente afín a *A. pressus* y *A. argentinus* (véanse diferencias bajo estas especies). Para una mayor aclaración de la variación morfológica y sinonimia véase Cialdella et al. (2006).

El material tipo de *Panicum hagenbeckianum* Kuntze, originalmente depositado en B, no pudo ser hallado y presumiblemente está destruído. En consecuencia, se designa al fragmento depositado en US (número 80689) como lectotipo de la especie por corresponderse totalmente con el protólogo de la misma.

Material adicional examinado. ARGENTINA. **Buenos Aires:** Pdo. Pergamino, Manuel Ocampo, *Parodi 49432* (BAA). **Chaco:** Dpto. Donovan, 13 km N de la Verde, Ea. Dos Tranqueras, *Schinini 22842* (BAA, CTES, SI). **Córdoba:** Marcos Juárez, *Stuckert 14813* (SI). **Corrientes:** Dpto. Mercedes, Colonia Itá Caabó, *Pedersen 6110* (BAA, CTES, US). **Entre Ríos:** Dpto. Federación, Santa Ana, *Guaglianone et al. 481* (MO, SI). **Formosa:** Las Palmas, *Jörgensen 2428* (MO, SI). **Misiones:** Dpto. Apóstoles, San José, Escuela Agrotécn. Don Bosco, *Renvoize 3042* (MO, SI, US). **Santa Fe:** Dpto. Castellanos, Ataliva, *Pire 1070* (MO, SI). BRASIL. **Paraná:** Serrinha, *Dusén 17669* (MO, SI, US). **Rio Grande do Sul:** Pelotas, *Costa Sacco 230* (BAA, F, US). **Santa Catarina:** Abelardo Luz, 8–12 km N of Abelardo Luz, *Smith & Klein 13338* (F, SI, US). PARAGUAY. **Alto Paraná:** Itaquyry, *Fiebrig 5689* (BAA, G, LIL, SI). **Amambay:** Sierra de Amambay, *Hassler 9729* (G). **Caaguazú:** Coronel Oviedo, *Pavetti Morín & Rojas 9993* (BAA, SI). **Canindeyú:** Camino Jejui-mi–Lagunita, Km 11, *Marín & Jiménez 636* (MO, SI). **Central:** Paraguaria centralis, in regione lacus Ypacaray, *Hassler 12556* (G, MO, US). **Cordillera:** Caacupé, Tobatí, *Nicora et al. 9901* (MO, SI). **Guairá:** Villarrica, *Rojas 9254* (BAA, LIL, SI). **Itapuá:** Yacyretá, *Zardini et al. 51634* (MO, SI). **Misiones:** Ea. La Soledad, *Pedersen 7633* (BAA, CTES, US). **Paraguarí:** Caápucú, Ea. Barrerito, orilla del Ayo. Yaguarí, *Ramírez 430* (BAA, LIL). **San Pedro:** Distr. Lima, Est. Carumbé, *Pedersen 8470* (CTES). URUGUAY. Canelones, cerca del Parque Racine, *Legrand 991* (BAA). **Cerro Largo:** Río Negro, Ea. Palleros, *Gallinal et al. 1235* (BAA, F, SI, US). **Durazno:** Ea. Las Palmas, *Schrader 18745* (US).

Florida: Timote, Santa Clara, *Gallinal et al. 3035* (US). **Paysandú:** Meseta de Artigas, Río Uruguay, *Rosengurtt 9283* (BAA, SI, US). **Rocha:** Cerro de los Indios, Rt. 16, *Rosengurtt 11189* (MO). **San José:** Barra Santa Lucía, *Rosengurtt 6615* (US). **Tacuarembó:** Gruta de los Cuervos, 11 km al N de Tacuarembó, *Morrone et al. 5271* (SI).

31. Axonopus uninodis (Hack.) G. A. Black, Advancing Frontiers Pl. Sci. 5: 102. 1963. Basiónimo: *Paspalum uninode* Hack., Ergebn. Bot. Exp. Sudbras. 1: 6. 1906. TIPO: Brasil. São Paulo: Pilar, betw. Alto da Serra & Santos, 1902, *M. Wacket s.n.* (holotipo, W!; isotipos, US 2856020!, US foto y fragm. en SI!, W fragm. en MO 3326814!, MO foto en SI!, W fragm. en SI!).

Paspalum plumosum Henrard, Meded. Rijks-Herb. 47: 1. 1922. *Axonopus plumosus* (Henrard) Henrard, Meded. Rijks-Herb. 47: 2. 1922. TIPO: Paraguay. Guairá: Cordillera de Villa Rica, 24 sep. 1874, *B. Balansa 105* (holotipo, L 908.93-857 no visto; isotipos, G!, G fragm. en US 2856021!, L fragm. en US 2856022!).

Axonopus kleinii L. B. Sm. & Wassh., Bradea 2(35): 244. 1978, syn. nov. TIPO: Brasil. Santa Catarina: Campo Alegre, Morro Iquererim, alpine campo, 1300–1500 m, 8 sep. 1956, *L. B. Smith & R. Klein 7432* (holotipo, US 2237569!, US foto en SI!; isotipos, HBR no visto, US fragm. en SI!).

Plantas perennes, cespitosas, cortamente rizomatosas; cañas erectas, de 20–70 cm de alto, comprimidas; entrenudos 1–3, de 20–35 cm, pajizos, lisos, glabros; nudos vilosos, con pelos largos o cortos, blanquecinos, adpresos. Vainas predominantemente basales, de 4–14 cm, estriadas, glabras, las inferiores largamente pilosas junto a la unión con la lámina, con pelos blanquecinos y sedosos, los márgenes membranáceos, glabros a pestañosos hacia la porción superior; lígulas membranáceo-ciliadas, de 0.3 mm, cuello ligeramente distinguible, glabro; láminas lineares, de 10–60 × 0.2–0.5 cm, rígidas, conduplicadas a involutas, glabras, de base estrecha, pilosas junto a la unión con la vaina, de ápice pungente, los márgenes membranáceos, pestañosos hacia la región basal. Inflorescencias terminales, de 5–12 × 1–3 cm, contraídas, exertas; pedúnculos de 20–50 cm, cilíndricos, glabros, lisos; eje principal anguloso, de 2–6 mm, surcado, glabro; racimos (2)3–4(–7), ascendentes, ligeramente divergentes, alternos, los superiores aproximados a conjugados; raquis de los racimos triquetro, de 40–85 × 0.3–0.7 mm, glabro, liso; pulvínulos glabros; pedicelos triquetros, de 0.3–0.6 mm, con los márgenes escabriúsculos. Espiguillas elipsoides, 4.2–4.8 × 0.9–1.1 mm, híspidas, con largos pelos blanquecinos hasta de 2.4 mm, distribuidos en la base y a lo largo de los márgenes, el resto de la superficie glabra; gluma superior y lema inferior subiguales, superando 0.4–1.2 mm en largo al antecio superior; gluma superior de 4–4.8 mm, 5(–7)-nervia, con los nervios manifiestos; lema inferior glumiforme, 5-nervia; antecio superior angostamente elipsoide, de 3–3.8 × 0.8–1 mm, pajizo, endurecido, finamente papiloso, de ápice agudo a subagudo, con un mechón de pelos rígidos, blanquecinos hacia el ápice de la lema; pálea de similar textura y ornamentación que la lema, glabra; lodículas 2, de 0.2–0.3 mm, cuneadas; estambres 3, anteras de 2.5–2.7 mm, purpúreas. Cariopsis no vista.

Hábitat y distribución. *Axonopus uninodis* posee una distribución restringida al sureste y sur de Brasil (Distrito Federal y estados de Santa Catarina y São Paulo) y noreste de Paraguay (Amambay). Crece en campos bajos y esteros o en campos abiertos, entre los 200 y 1500 m.s.n.m.

Nombre vulgar. "Grama-do-descampado" (Brasil, Smith et al., 1982: 1101 sub *Axonopus kleinii*).

Discusión. *Axonopus uninodis* pertenece a la serie *Barbigeri* por tener gluma superior y lema inferior con nervios manifiestos y antecio superior pajizo. Dentro de esta serie, *A. uninodis* es morfológicamente afín a *A. comans*, distinguiéndose esta última por tener la gluma superior y la lema inferior glabras o esparcidamente pilosas entre los nervios (vs. espiguillas con gluma superior y lema inferior híspidas, cubiertas de pelos blanquecinos hasta de 2.4 mm), láminas filiformes, macizas (vs. láminas lineares, no macizas) y cañas con nudos glabros (vs. cañas con nudos vilosos en *A. uninodis*).

Zuloaga y Morrone (2003) tratan a *Axonopus kleinii* bajo la sinonimia de *A. marginatus*. El análisis del ejemplar tipo de *A. kleinii* permitió determinar que el tamaño de las espiguillas, de 4 mm de largo, y el tipo de nerviación de la gluma superior y lema inferior (5-nervias), con los nervios conspicuamente marcados y con el nervio medio desarrollado, se corresponden con *A. uninodis*; por tal motivo en el presente trabajo se trata a *A. kleinii* bajo la sinonimia de *A. uninodis*.

Mez (1917) al describir *Paspalum proximum* cita dos sintipos, *Balansa 69* (G-Bois.!, K!, P!, US!) y *Hassler 11382* (F!, G!, MO!). Chase y Niles (1962) observaron que ambos sintipos correspondían a dos especies diferentes y seleccionaron el ejemplar *Balansa 69* como lectotipo de *P. proximum* Mez (= *P. ellipticum* Döll), identificando al restante sintipo como *Axonopus comans*. El estudio de ejemplares de *Hassler 11382* depositados en los herbarios G y MO permitió determinar que los mismos corresponden a *A. uninodis* (y no a *A. comans*, por tener estos ejemplares espiguillas híspidas, láminas lineares, no macizas y nudos vilosos).

Material adicional examinado. BRASIL. **Distrito Federal:** Brasília, *Irwin et al. 10611* (MO). PARAGUAY. **Amambay:** Sierra de Amambay, *Hassler 11382* (F, G, MO); Estero Ypayeré, *Rojas 6390* (BAA, MO); Cerro Torin, *Rojas 3994* (BAA); in altaplanitie Sierra de Amambay, *Hassler 11382b* (G).

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Apéndice 1. Lista de especies estudiadas.

1. *Axonopus andinus* G. A. Black
2. *A. argentinus* Parodi
3. *A. aureus* P. Beauv.
4. *A. boliviensis* Renvoize
5. *A. brasiliensis* (Spreng.) Kuhlm.
6. *A. capillaris* (Lam.) Chase
7. *A. caulescens* (Mez) Henrard
8. *A. chrysoblepharis* (Lag.) Chase
9. *A. comans* (Trin. ex Döll) Kuhlm.
10. *A. compressus* (Sw.) P. Beauv.
11. *A. cuatrecasasii* G. A. Black
12. *A. equitans* Hitchc. & Chase
13. *A. fissifolius* (Raddi) Kuhlm.
14. *A. flabelliformis* Swallen
15. *A. herzogii* (Hack.) Hitchc.
16. *A. hirsutus* G. A. Black
17. *A. iridifolius* (Poepp.) G. A. Black
18. *A. kuhlmannii* G. A. Black
19. *A. leptostachyus* (Flüggé) Hitchc.
20. *A. marginatus* (Trin.) Chase ex Hitchc.
21. *A. obtusifolius* (Raddi) Chase
22. *A. pellitus* (Nees ex Trin.) Hitchc. & Chase
23. *A. polystachyus* G. A. Black
24. *A. pressus* (Nees ex Steud.) Parodi
25. *A. purpusii* (Mez) Chase
26. *A. rosengurttii* G. A. Black
27. *A. scoparius* (Flüggé) Kuhlm.
28. *A. siccus* (Nees) Kuhlm.
29. *A. succulentus* G. A. Black
30. *A. suffultus* (J. C. Mikan ex Trin.) Parodi
31. *A. uninodis* (Hack.) G. A. Black

Apéndice 2. Índice de coleccionistas. Cada espécimen es citado por el nombre del primer colector cuando otros coleccionistas participan de la colección. Se indica entre paréntesis el número de orden de la especie (véase Apéndice 1).

Abrell 32 (13); *Alonso 196* (30); *Anderson 1128* (10), *7749* (6); *Antezana 1251* (28); *Araujo 12* (20), *31* (20), *33* (2), *61* (2), *67* (20), *85* (30), *102* (2), *146* (28), *161* (28), *175* (2); *Arbo 1083* (30), *6951* (30), *8407* (10); *Archer 4619* (10), *4818* (10), *4830* (30); *Arechavaleta s.n.* (2); *Arenas 11* (13).

Bacigalupo 558 (30), *782* (13), *865* (13), *986* (13), *1043* (30); *Baez 27* (2), *s.n.* (2); *Balansa 93* (13), *95* (28), *96* (28), *97* (2), *99* (30), *104* (9); *Bang 872* (6); *Barreto 48* (13), *1317* (2), *1358* (30), *4689* (30); *Bastián 1313* (28); *Bazzi 14* (30), *401* (30); *Beck 2195* (27), *3225* (13), *3374* (3), *3388* (10), *3493a* (10), *3493b* (10), *3650* (27), *5134* (19), *5210* (4), *5395* (19), *5683* (13), *5803* (10), *9913* (3), *9934* (28), *10108* (3), *12323* (8), *13379* (27), *14811* (3), *14819* (28), *14964* (3),

15183 (19), *15193* (19), *16255* (27), *16256* (28), *17110* (10), *17182* (27), *17190* (3), *17469* (28), *17548* (6), *17602* (28), *17605* (3), *17852* (20), *18414* (8), *18510* (3), *18511* (14), *18615* (17), *18634* (10), *19935* (17), *20620* (5), *21085* (8), *22399* (27), *23569* (13), *23935* (28), *24134* (5), *24199* (8), *25703* (8), *27215* (13); *Beetle 1190* (28), *1570* (13), *1580* (13), *1689* (13), *1939* (13); *Biganzoli 283* (30), *340* (30), *1329* (10); *Böher 2371* (10); *Bonifacino 1976* (2); *Bordas 1145* (10); *Bresia 4156b* (28); *Bresolin 158* (5), *1165* (21), *1194* (21); *Bruderreck 55* (25), *67* (28), *138* (13), *234* (4), *299* (8); *Brunner 1055* (13), *1056* (13); *Buchtien 2* (27), *12* (14), *27* (6), *448* (17), *5324* (27), *6324* (27), *6434* (13), *7118* (20), *7142* (3), *s.n.* (13); *Bueno 2284* (28); *Burkart 816* (2), *824* (2), *1215* (13), *1257* (10), *3476* (13), *3718* (13), *4158* (13), *7593* (10), *7938* (30), *10580* (13), *11231* (28), *11361* (28), *12831* (10), *12901* (10), *14009* (10), *14190* (10), *14304* (30), *14350* (30), *17759* (10), *18402* (13), *18566* (30), *19425* (30), *19674* (10), *19725* (10), *20652* (10), *20901* (10), *21022* (13), *21022* (13), *21023* (2), *21024* (10), *21025* (10), *21025 (b)* (13), *22908* (10), *22922* (2), *22929* (30), *23253* (13), *24062* (13), *24078* (2), *24710* (13), *24728* (30), *25269* (2), *25270* (2), *26188* (13), *26192* (30), *26193* (2), *26205* (2).

Cabrera 26127 (10), *27310* (13), *27349* (10), *28146* (30), *28268* (2), *28410* (30), *28480* (10), *28728* (30), *30462* (10), *34238* (13), *34320* (10), *34796* (10); *Calderón 477* (13); *Cárdenas 3608* (28); *Carnevali 4426* (10), *5562* (10); *Caro-Rojas 1553* (10); *Cialdella 389* (28); *Clayton 4313* (30); *Cocucci 3078* (30); *Conrad 2213* (13); *Cordeiro 905* (15); *Costa Sacco 230* (30), *280* (10), *393* (28); *Crovetto M. 2209* (13); *Cusato 1178* (2), *s.n.* (30); *Cutler 7018* (15), *9088* (28).

D'Arcy 13901 (27); *Daly 2177* (15); *Dauber 111* (2); *Davidse 1985* (3), *10968* (28), *10973* (13), *10986* (5), *11034* (22), *11049* (23), *11118* (28), *11128* (28), *11133* (28), *11257* (10), *11285* (28), *11300* (28), *11311* (22), *11326* (13), *11377* (24), *13076* (17); *de Llamas s.n.* (2); *Deginani 83* (10), *92* (10), *133* (10), *377* (28), *1452* (10); *Del Mazo 12383* (2), *s.n.* (2); *Diers L. 359* (10); *Dombrowski 2262* (10), *2268* (10), *4353* (30); *Dusén 2523* (9), *3934* (24), *11686* (24), *13274* (5), *14502* (28), *15073* (28), *16025a* (20), *16048* (9), *16836* (8), *16838* (8), *17669* (30), *s.n.* (24), *s.n.* (28); *Dutra 423* (10), *466* (30), *466-A* (28), *556* (13).

Eskuche 2528–8 (2).

Felippone 5363 (30); *Fernándes 71* (28), *499* (10); *Ferrucci 1393* (13), *6347* (30); *Feuerer 5838* (27); *Fiebrig 120* (28), *783* (28), *4603* (28), *4694* (5), *4779* (13), *4910* (25), *5003* (13), *5048* (8), *5101* (28), *5178* (28), *5191* (8), *5374* (30), *5581* (10), *5689* (30), *5709* (28), *5791* (8), *6735* (30); *Fontana F-111-6* (2), *F-180-2* (10), *F-180-36* (30), *F-201-12* (13), *F-204-5* (19), *F-253-4* (30), *F-254-10* (10), *F-258-1* (10); *Franceschi 623* (10); *Fredholm 5255* (13); *Fuentes 450* (28), *2182* (28), *2893a* (24), *5793* (20).

Galli 54 (2), *243* (10), *287* (2); *Gallinal 1235* (30), *1491* (2), *1499* (2), *1812* (2), *1937* (2), *1947* (2), *2081* (2), *2735* (2), *2907* (2), *3035* (30), *3585* (2), *3991* (2); *García 28* (3), *29* (28); *Gattoni 13359* (2); *Giambiagio s.n.* (13); *Giberti 69* (10), *72* (10); *Gilberto 1613* (10); *Giraldo-Cañas 2802* (28), *2803* (28); *Giusti 1964* (10); *Gonzales 3733* (18), *4459* (15), *4943* (28), *5052* (3); *Guaglianone 481* (30); *Guillén 872* (20), *1116* (28), *2736* (13), *4790* (5); *Gutiérrez 1194* (5), *1372* (15), *1551* (28), *1565c* (3), *1810* (3).

Haase 172 (3), *187* (3), *291* (6), *626* (19), *627* (18); *Hanagarth 97* (20), *150* (20), *232* (20); *Hartley SH-158* (2); *Hassler 37* (28), *70 bis* (10), *71* (13), *1621* (10), *1691* (10), *2069* (13), *2070* (10), *8035* (13), *8248* (25), *8311* (28), *9269* (24), *9269a* (24), *9729* (30), *10171* (28), *10381* (28), *10747* (8), *10781* (25), *10788* (5), *11382* (31), *11382b* (31), *11548* (28), *11645* (25), *11942* (9), *11973* (5), *12556* (30), *13031* (2); *Hatschbach 2949* (23), *3568* (30), *4178* (30), *6866* (24), *8924* (28), *9078* (24), *14010* (24), *14013* (24), *16179* (28), *28600* (21), *30493* (28), *30691* (2), *30766* (30), *33649* (21), *35864* (13), *38067* (28), *40445* (9), *43506* (28), *43557* (23), *43564* (10), *44342* (20), *44552* (3), *44605* (28), *45704* (5), *59112* (28); *Hebert s.n.* (13); *Henz 35506* (13), *35657* (30); *Herbert 20777* (13); *Hertel 2467* (24); *Herter 332* (10); *Hitchcock 22657* (6); *Hoc 158* (30); *Holst 4669* (10); *Hunziker 11050* (10).

Ibarrola 1880 (13); *Ibisch 1305-L-030* (3); *Insfrán s.n.* (13).

Jackson s.n. (13); *Jiménez 29* (19), *140* (24), *1177* (28), *1203* (3), *1242* (28), *2043* (24), *13509* (28), *14638* (19), *14665* (30), *14675* (19), *14677* (10), *14655 1/2* (30), *1978BJ* (10); *Job 712* (10), *760* (2); *Jörgensen 2428* (30), *3529* (10), *3538* (10), *3548* (10), *4101* (30).

Killeen 556 (10), *611* (13), *630* (3), *642* (13), *674* (13), *686* (3), *696* (3), *705* (28), *753* (28), *773* (13), *860* (3), *874* (8), *894* (8), *928* (11), *968* (10), *1138* (20), *1200* (20), *1347* (13), *1389* (20), *1402* (5), *1518* (28), *1531* (25), *1576* (16), *1577* (11), *1603* (3), *1624* (13), *1629* (3), *1633* (19), *1663* (28), *1668* (3), *1680* (10), *1685* (19), *1725* (11), *1751* (10), *1804* (3), *1839* (28), *1849* (8), *1957* (8), *1976* (28), *1982* (3), *1992* (8), *2011a* (8), *2113* (8), *2229* (20), *2253* (25), *2262* (28), *2266* (28), *2275* (13), *2290* (11), *2297* (16), *2381* (28), *2383* (3), *2399* (28), *2456* (8), *2490* (28), *2591* (8), *2788* (5), *2789* (20), *2818* (8), *2819* (28), *2834* (5), *4799* (5), *4830* (3), *5725* (5), *6040* (28), *6476* (8), *6539* (18), *6627* (15), *7036* (20), *7043* (20), *7051* (5), *7159* (20), *7242* (5), *7360* (13), *7443* (8), *7471* (15), *7725* (5), *7732* (20); *Klein 121* (10), *3549* (30), *3609* (2), *3657* (30), *3729* (30), *3798* (30), *4172* (10), *10432* (10), *10631* (10), *11167* (10), *11329* (21), *11335* (21), *11342* (21), *11512* (21), *11665* (10), *11672* (10), *12029* (10), *12074* (13), *12129* (13), *12136* (10), *12162* (10), *12174* (10); *Krapovickas 6863* (6), *12272* (2), *13923* (28), *14266* (24), *16961* (10), *17098* (10), *22309* (10), *22800* (13), *23279* (28), *24110* (10), *24253* (19), *29238* (10), *31704* (13), *31746* (8), *32086* (8), *32483* (13), *32493* (13), *36159* (8), *36216* (13), *44594* (30), *45864* (5); *Kressler 114* (3); *Kuhlmann 1712* (16), *1722* (15); *Kummrow 1466* (28), *1696* (23), *1742* (28), *1835* (28); *Kuntze s.n.* (30).

Lanfranchi 1335 (10); *Lara & Culle 1634* (10); *Legrand 991* (30); *Lewis 582* (30), *784* (30), *949* (10), *1062* (30), *1470* (30); *Lindeman 4689* (28), *s.n.* (13); *Lipa 34* (13); *Lombardo 3032* (2); *Longhi-Wagner 3794* (10), *3828* (5), *9087* (5), *9410* (3), *9425* (28), *9432* (13), *9439a* (28), *9457* (22), *9459* (28), *9461a* (5), *9467* (13), *9468* (24), *9480* (20); *López 207* (24), *385* (27), *386* (1); *Lourteig et al. 2911* (30).

Maldonado 3023 (3), *3056* (20); *Marín 636* (30), *GM-636* (30); *Martínez s.n. (BAA 9677)* (30); *Martínez Crovetto 3365* (2), *6294* (30), *9940* (2); *Mattos 7290* (30); *Menacho 333* (11), *478b* (8); *Mereles 3567* (28); *Meyer 32* (2), *67* (30), *89* (30), *367* (30), *373* (13), *15450* (10), *15452* (10), *18019* (10), *s.n.* (30); *Michel 2059* (5); *Miranda 190* (7), *252* (20), *320* (20), *570* (7), *732* (14), *733* (28), *808* (28), *809* (7), *824* (7), *832 p.p.* (3), *833* (7), *844* (28), *858* (7), *1835* (20); *Montes 102* (13), *2217* (13), *10827* (30), *11083* (13), *12725* (30), *12834* (2), *15230* (30), *15251* (13), *15265* (10), *15272* (30), *15280* (10), *15283* (2), *15339* (10), *15352* (13), *15442* (2), *15650* (10), *16160* (10), *16237* (10), *16313* (10), *16337* (10), *16437* (30), *16442* (2), *16460* (10), *27647* (28); *Morel 9012* (30); *Morello 510* (10), *533* (10); *Morrone 114* (2), *190* (13), *195* (13), *224* (13), *316* (13), *347* (13), *381* (24), *394* (24), *425* (13), *425a* (24), *432* (24), *461* (13), *463* (24), *467* (28), *471* (28), *493* (13), *515* (28), *522* (28), *539* (28), *548* (5), *557* (28), *559* (25), *562* (13), *684* (10), *720* (10), *722* (21), *990* (28), *1082* (28), *1411* (10), *1488* (13), *1592* (30), *1604* (20), *1709* (20), *1711* (20), *1751* (30), *1767* (30), *1785* (13), *1817* (30),

1830 (10), *2312* (28), *3687* (13), *3776* (28), *4209* (27), *4283* (10), *4296* (20), *4303* (25), *4305* (13), *4413* (28), *4821* (27), *4832* (27), *4841* (28), *4843* (17), *4845* (3), *4888* (27), *4904* (1), *4956* (8), *4968* (28), *4977* (19), *4983* (4), *5004* (10), *5040* (4), *5042* (25), *5062* (4), *5075* (19), *5271* (30), *5292* (2), *5342* (2), *5375* (9), *5378* (5), *5380* (20), *5384* (21); *Mostacedo 187* (10), *222* (17), *238* (11), *490* (28), *777* (20), *1396* (3), *1520* (3), *1655* (3), *1880* (24), *2483* (13), *2666* (11), *2926* (11), *1563A* (6); *Múlgura de Romero 1662* (30), *1672* (10), *2170* (30), *2373* (10), *2479* (30), *2501* (10), *2796* (10), *2823* (30); *Müller 9105* (28).

Narel Paniagua 789 (28); *Nee 34652* (19), *36379* (11), *41480* (4), *42172* (13), *44832* (10), *48542* (27), *48547* (27); *Nicora 517* (2), *571* (2), *2985* (13), *3071* (2), *4526* (13), *4701* (28), *4755* (13), *5746c* (2), *8725* (10), *9872* (10), *9901* (30), *s.n.* (13); *Norrmann 155* (24); *Nutz 12* (10).

Oliveira 137 (3), *304* (28), *561* (3), *563* (19), *624* (19), *638* (19); *Orihuela 63* (2), *300* (2); *Orth 743* (13), *s.n.* (30); *Osten 7380* (28).

Parodi 11 (30), *63* (30), *151* (26), *157* (2), *157 1/2* (2), *547* (26), *4094* (30), *4187* (2), *4326* (30), *4632* (2), *4780* (30), *4942* (30), *5283* (2), *5645* (30), *5701* (2), *5805* (2), *6135* (30), *6191* (2), *6294* (2), *6359* (2), *6790* (30), *9593* (2), *10633* (13), *11203* (30), *15282* (26), *49432* (30); *Pavetti Morín 686* (10), *3586* (10), *9993* (30); *Pedelaborde s.n.* (2); *Pedersen 1011* (2), *1338* (30), *1387* (13), *3638* (2), *4255* (30), *4291* (10), *4482* (2), *4712* (2), *5531* (19), *5829* (2), *5876* (2), *6110* (30), *6426* (2), *7024* (10), *7568* (10), *7614* (13), *7633* (30), *8393* (30), *8470* (30), *8502* (5), *8708* (19), *9600* (2), *11051* (28), *11498* (30), *12993* (10), *13508* (10), *13509* (13), *13511* (10), *13770* (10), *13880* (28), *14833* (13), *15144* (13), *15578* (2), *15694* (28), *15772* (10), *15894* (28); *Pensiero 149* (10), *520* (2), *2564* (10), *2798* (10), *2998* (30), *4550* (13), *4644* (10), *6843* (10), *6885* (30), *6887* (10), *6894* (30), *6993* (10), *6994* (13); *Pinto s.n.* (28); *Pire 1070* (30); *Polanco 157* (13); *Poliquesi 74* (5); *Porta 69* (10), *102* (30); *Pott 943* (10).

Quarín 220 (10), *428* (10), *569* (21), *869* (2), *1025* (10), *1178* (10), *1578* (10), *1591* (13), *1664* (30), *1694* (30), *1850* (2), *2442* (10), *2489* (10), *2659* (30), *2838* (30), *2959* (30), *3451* (10), *3495* (20), *4137* (2); *Quintana 1* (10), *73* (10).

Ragonese 2712 (30), *2801* (30), *25939* (13); *Rambo 4792* (10), *29048* (10), *29313* (2), *30763* (30), *35153* (2), *36459* (2), *43592* (30), *44003* (30), *44092* (30), *45409* (30), *53411* (30), *56010* (30), *56320* (30); *Ramírez 407* (30), *428* (10), *430* (30), *649* (2); *Reitz 2633* (2), *3269* (30), *3300* (10), *7798* (30), *11612* (30), *12631* (30), *14147* (2), *17681* (30); *Renvoize 2995* (30), *3042* (30), *3934* (3), *3943* (16), *3947* (11), *3959* (27), *3991* (3), *3994* (11), *4029* (11), *4261* (27), *4263* (1), *4603* (8), *4607* (28), *4678* (13), *4680* (10), *4706* (3), *4714* (13), *4719* (28), *4730* (27), *4740* (17), *4759* (3), *4760* (28), *4775* (27); *Rodriguez 471* (5), *573* (30), *710* (10); *Rojas 1037* (28), *2304* (30), *2786* (13), *3994* (31), *4822* (28), *4830* (30), *5112* (24), *5254* (2), *5259* (28), *5415* (10), *5432* (2), *5804* (10), *6390* (31), *6537* (20), *6675* (28), *6704* (2), *6716* (24), *6716a* (24), *6749* (24), *6770* (28), *6826* (28), *6872* (24), *7390* (13), *7888* (28), *7964* (30), *7995* (13), *8761* (28), *8770* (28), *9254* (30), *9254a* (30), *9519* (28), *9600* (13), *10330* (10), *10366* (28), *10532* (13), *10880* (10), *12702* (13), *12702a* (13), *12716* (10), *12812* (13), *12826* (13), *12893* (10), *13103* (10), *13129* (2), *13135* (13), *13197* (2), *13202* (2), *13203* (2), *13264* (28), *13272* (13), *13363* (13), *14076* (2), *14105* (2), *14156* (30), *14187* (13), *14197* (30), *14234* (13), *14345* (10), *14526* (13), *14587* (13), *135-1030* (3); *Romanczuk 119* (2), *174* (10); *Rosa-Mato 1463* (2); *Rosengurtt 305* (2), *1063* (2), *1210* (10), *5356* (13), *5366* (10), *5377* (10), *5409* (13), *5441* (13), *5536* (10), *6615* (30), *9283* (30), *11189* (30), *B-282* (13), *B-588* (2), *B-715* (2), *B-795* (10), *B-825* (2), *B-955* (2), *B-5335* (30), *B-5356* (13), *B-5389* (13), *B-5391* (2), *B-5409* (13), *B-5441* (13), *B-5780* (28), *B-5871* (28), *B-6161* (28), *B-6435 1/2* (30), *B-7029* (28), *B-7073* (28), *B-7406* (2), *B-9189* (30), *PE-3422* (21); *Rotman 655* (10); *Rua 38* (2), *123* (24), *138* (30), *404* (3); *Rúgolo 1211* (10), *1438* (10), *1573* (10), *1587* (10), *1629* (30), *1632* (10), *1640* (10), *1720* (28), *1733* (5), *1779* (10), *1784* (21), *1792* (10), *1956* (3), *2052* (13), *2066* (10); *Rusby 241* (6).

Sacco 2363 (20); *Saldias 5007* (8); *Saravia 513* (28); *Saravia Toledo 11695* (13), *12324* (28); *Sarli 101* (2); *Schinini 1421* (10), *1548* (10), *5873* (10), *6046* (10), *6218* (13), *6242* (13), *7045* (10), *7049* (10), *7969* (10), *8552* (10), *10519* (30), *10560* (30), *12361* (2), *13157* (13), *13779* (19), *14407* (10), *14606* (2), *15437* (19), *15665* (30), *16084* (10), *17547* (13), *19324* (19), *19401* (13), *21497* (5), *22842* (30), *25068* (10), *26752* (13), *28245* (30), *28545* (24), *30059* (30), *34411* (28), *35815* (28), *36028* (28); *Schoppenhorst B-531* (3); *Schrader 18745* (30); *Schultz 3269* (2), *3326* (2), *3628* (30), *3687* (30), *3808* (30), *11040* (2), *11677* (13), *11786* (2), *17328* (10); *Schwarz 6310* (30), *6379* (30), *6581* (30), *8073* (30), *8154* (30); *Sehnem 4249* (2); *Seidel 400* (28), *401* (8), *409* (8), *411* (24), *490* (10), *892* (27), *978* (3), *999* (27), *2081* (10), *2364* (10), *2856* (10), *7524* (10), *7791* (10); *Seijo 261* (30), *2528* (2); *Simas 35457* (30). *Sine coll. 497* (21), *4358* (13), *16324* (13), *s.n.* (2); *Single MS-18* (19); *Smith 1000* (14), *7405* (5), *8053* (2), *8237* (2), *8629* (2), *9039* (30), *9307* (30), *10306* (30), *12839* (30), *13338* (30), *13820* (30), *13861* (30), *13990* (2), *14064* (30), *14109* (10), *14755* (23), *15473* (30), *15506* (10), *15623* (24), *15644* (30), *15688* (10), *16039* (2); *Solomon 6926* (24), *7071* (24), *8521* (10), *13708* (27), *16819* (10), *18509* (1), *18807* (27), *18835* (3), *18836* (28), *18850* (1), *18850 (B)* (7); *Soria 5982* (24); *Sparre 388* (13), *1040* (10), *1523* (28), *2209* (13); *Steinbach 1920* (28), *1979* (11), *5159* (10), *5377* (28), *5426* (3), *6847* (13), *6948* (3), *6976* (28), *6990* (10); *Stuckert 14813* (30); *Swallen 6999* (3), *7096* (10), *7188* (30), *7226* (30), *7463* (2), *7544* (2), *7544A* (2), *7630* (30), *7638* (2), *7718* (2), *7765* (10), *8110* (2), *8181* (30), *8221* (2), *8250* (10), *8258* (10), *8308* (28), *8320* (30), *8409* (10), *8414* (10), *8478* (5), *8569* (23), *8586* (10), *8649* (23), *8661* (24), *8662* (24), *8664* (22), *8672* (24), *8820* (10), *8832* (20), *8910* (10), *8968* (24), *8976* (24), *8986* (24), *8988* (24), *9023* (24), *9169* (2), *9442* (20), *9458* (13), *9513* (10).

Tarifa 5021 (27); *Tata 429* (27); *Tejada 58* (8); *Tressens 1081* (30), *1457* (30), *1855* (30); *Troncoso 1617* (10), *2464* (13), *2504* (30), *2696* (30), *3386* (2); *Türpe 2357* (10).

Uslar 659 (3).

Valls 72 (30), *85* (20), *206* (21), *931* (*10*), *936* (13), *1105* (13), *2534* (10), *14194* (10), *14299* (21), *s.n.* (28); *Vargas 401* (28), *2035* (27); *Venturi 2* (30), *1708* (13), *2384* (30), *7879* (13), *9845* (13), *10032* (28); *Villalobos 313* (10); *Villamil 3096* (13).

Wood 7864 (28), *9623* (27), *10805* (17), *10946* (28), *12179* (11), *13443* (11), *14327* (25), *14758* (8), *14809* (3), *15427* (20), *17198* (28); *Woolston 55* (13), *106* (13), *G-73 pro parte* (30), *G-77* (30).

Zardini 10241 (10), *11827* (2), *15970* (30), *16135* (10), *17308* (13), *19386* (13), *19836* (13), *19839* (13), *21866* (10), *23522* (10), *23694* (10), *23820* (30), *23845* (10), *24015* (10), *24075* (30), *24518* (10), *24676* (10), *24733* (10), *24738* (30), *25054* (10), *25200* (10), *26089* (28), *26188* (28), *26254* (28), *38573* (13), *47439* (10), *48288* (24), *51634* (30), *52959* (10), *53693* (28), *53733* (28), *53776* (28), *55323* (10), *55913* (30); *Zuloaga 446* (30), *476* (10), *503* (30), *2982* (10), *3102* (30), *3175* (19), *3449* (28), *4923* (28), *5324* (28), *5511* (10), *5598* (10), *5858* (28), *6144* (28), *6158* (10), *6430* (30), *6458* (30), *6551* (30), *6655* (10), *6811* (28), *7126* (30), *7196* (30), *7257* (13), *7262* (24), *7283* (13), *7632* (28).

AFRICAN HERBARIA SUPPORT TRANSFORMATION ON THE CONTINENT[1]

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Abstract

The African Plants Initiative (API) was conceived as a web-based, electronic venture that would provide rapid access to images of type specimens of African plant names. This soon grew to also encompass images of living plants, associated taxonomic literature, artwork, and related texts. In many respects, Africa, which is host to a flora of over 50,000 species, for which about six times that number of alternative and incorrect names are available, has historically lagged behind the world in terms of both taxonomic capacity and access to the global electronic ether. Through the API, a consortium of 73 institutions from the North and South, 291,289 specimen images alone are now available for accessing through the Internet. In this regard, the API has been a pioneer in and has become a catalyst for facilitating the generation and dissemination of fundamental taxonomic information on African plants, a role it is increasingly fulfilling through the JSTOR Plant Science portals.

Key words: Africa, herbaria, North-South and South-South collaboration, specimens, taxonomy.

Herbaria, as archives and repositories for a country's or region's plant diversity, are vital for taxonomists who catalogue plant and genetic diversity and associated data. This information is useful for a wide array of end-users, such as conservationists, plant breeders, geneticists, phytochemists, ecologists, plant physiologists, human health officials, and ethnobotanists (Steenkamp & Smith, 2003). Although biological taxonomy is known for its classical and conservative roots, the electronic age has indeed proven to provide a variety of suitable vehicles for disseminating primary biodiversity information (Wheeler et al., 2004; Smith et al., 2007). In executing their duties, taxonomists are therefore nowadays increasingly making use of modern technologies to expedite service delivery.

The concept of having a type specimen permanently associated with a plant name was first introduced at the Fifth International Botanical Congress (IBC), which was held in the United Kingdom, at Cambridge, in 1930. A nomenclatural type (or typus) is defined as "...that element to which the name of a taxon is permanently attached, whether as a correct name or as a synonym" (McNeill et al., 2006: Art. 7.2). This element for extant plants may be one or more than one individual plant specimen(s), from a collector's single gathering, permanently preserved on one or more herbarium sheets. Therefore, as long as the type concept in modern plant nomenclature is followed by plant taxonomists, type specimens will remain of paramount importance as one of the primary sources of information in plant diversity investigations. In this regard, they also authenticate and document the taxon in scientific rigor. It is therefore not surprising that in December 2003 the African Plants Initiative (API) began with its primary objective to create high-resolution electronic images of as many type specimens of names published for African plants as possible, and to make these images and their associated metadata broadly available electronically to a global scholarly community (Smith, 2004; Demissew et al., 2005). Presciently, at the Fifth IBC, Harvey Hall proposed the making and distribution of photographs of types and producing an index to collections in different herbaria, suggestions that coincide with the primary objective of the API (Brooks & Chipp, 1931).

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This objective to create electronic images of type specimens of African plant names and to disseminate them electronically has now largely been achieved through collaboration among a consortium of African and northern, mostly European and American, botanical institutions holding significant collections of type specimens of African plants (Table 1). Currently, 291,289 images of specimens digitized for the API are available in JSTOR Plant Science (<http://plants.jstor.org>), as originating from Aluka (Aluka, 2009). Twenty African herbaria participated in this initiative and have contributed images of 51,822 specimens, which is ca. 18% of the total number of African specimen images accessible on the Internet via the JSTOR Plant Science portal (<http://www.aluka.org>). Over 70% of the images for African taxa come from South African herbaria. Projects are now underway to increase the participation of herbaria from other African countries, with a small grants program supported by the Andrew W. Mellon Foundation having been launched to enable this. Images and associated metadata generated by participants in the API remain the property of participating institutions, but are now also disseminated through JSTOR Plant Science, an online environment, which is part of ITHAKA, a not-for-profit organization that aims to provide online access to an archive of international scholarly resources (<http://www.ithaka.org>).

The API, however, did not intend to stop at scanning and disseminating images of type specimens. What started out as a purely taxonomic project soon emerged as a major initiative that can also be used to provide other, related information on plant diversity through the Internet. The preparation of electronic images of botanical artifacts is therefore only the first step in a process that has now developed into an indispensable electronic resource on African plants. The success of the API is a clear manifestation of the willingness of African herbaria to collaborate with their northern and southern colleagues. This drive is facilitating the sharing of plant diversity information and the rapid and affordable dissemination thereof. By expediting this, African herbaria will enable their taxonomists, who are confronted by an immensely rich flora of over 50,000 species (Klopper et al., 2006), to overcome the digital divide and misconceptions about their ability to contribute in a meaningful way through embracing new technologies.

A further significant contribution of the API is that broader environmental issues that have become the subject of dialogue between African and northern herbaria can now be addressed. In this regard, it supports the principles of the New Partnership for Africa's Development (NEPAD, 2004), which aims, among other things, to "1) anchor the development of Africa on its resources and resourcefulness of its people; 2) establish partnerships between and amongst African peoples; 3) accelerate regional and continental integration; and 4) build the competitiveness of African countries and the continent." Clearly, Africa is ready to assume responsibility for its own future and to combine its strengths in natural resources studies and to draw on its own innate abilities to manage these resources wisely for the benefit of all its peoples, indeed, for the benefit of the global village.

It is very encouraging that plant diversity sciences have attracted the support of the Andrew W. Mellon Foundation as a supportive partner in helping Africa to tackle some of the impediments that resulted from decades of exploitation, civil wars, corruption, and political maladministration. These impediments seriously impact the ability of many African countries that are signatories to the Convention on Biological Diversity (CBD) to respond to challenges presented to them.

As Africa takes another firm step toward developing a continent that can take its rightful place in the global arena, the API clearly acts as a catalyst to drive related scientific activities. Indeed, thanks to the API, African plant scientists now have an opportunity to mobilize their human power, resources, and infrastructure on an unprecedented scale. As with most, if not all, broad initiatives with the scope and dimensions of the API, progress is made in a stepwise manner. These steps, however, should be taken with the goal in mind to sustainably take ownership of the initiative and provide African taxonomists with the tools and knowledge to contribute toward, to manage, and to disseminate appropriate plant diversity information on the African flora. This sharing of information among participating countries, and ultimately with the broader botanical community, already contributes to a better understanding of the continent's significant botanical diversity, for example, through recent work conducted on the plant diversity of Angola (Figueiredo & Smith, 2008; Figueiredo et al., 2009; Smith & Figueiredo, 2010) and the continent's lycophyte and fern flora (Roux, 2009). Such improved knowledge should further stimulate renewed interest in the documentation of the continent's botanical wealth that is imperiled by human pressures. This essential and primary knowledge is vital if the natural resources of Africa are to be managed sustainably.

Table 1. African Plant Initiative partner herbaria (abbreviations follow Thiers, 2009) arranged according to the number of images submitted through the African Plant Initiative, the number of specimens imaged and uploaded to Aluka (2009), and the continents where located.

Herbarium	No. of specimen images uploaded	Continent	Total from continent
PRE	12,555	Africa	51,822
BOL	11,876	Africa	
NBG	4797	Africa	
NU	3853	Africa	
FHI	3163	Africa	
EA	2817	Africa	
SAM	2621	Africa	
GRA	2417	Africa	
GC	1612	Africa	
NH	1166	Africa	
RAB	1101	Africa	
YA	935	Africa	
IFAN	908	Africa	
TAN	693	Africa	
TEF	567	Africa	
ETH	379	Africa	
MHU	245	Africa	
KAW	60	Africa	
PRU	49	Africa	
SRGH	8	Africa	
K	59,821	Europe	231,171
P	48,232	Europe	
BR	20,884	Europe	
BM	17,374	Europe	
MPU	13,991	Europe	
B	9258	Europe	
S	8204	Europe	
G	7628	Europe	
M	7000	Europe	
HBG	3993	Europe	
FT	3868	Europe	
E	3786	Europe	
LISC	3096	Europe	
WAG	3038	Europe	
TCD	2481	Europe	
W	2126	Europe	
C	1808	Europe	
L	1523	Europe	
LISU	1435	Europe	
JE	1348	Europe	
COI	1326	Europe	
LD	1201	Europe	
G-DC	1019	Europe	
MA	962	Europe	
FI	940	Europe	
GOET	882	Europe	
HEID	807	Europe	
BC	764	Europe	
WU	521	Europe	
FR	467	Europe	
STU	466	Europe	
HAL	283	Europe	
KW	150	Europe	
U	138	Europe	
CGE	130	Europe	
AIX	99	Europe	
GZU	79	Europe	
MSB	30	Europe	
H	13	Europe	
MO	4509	North America	8,296
NY	1513	North America	
US	1022	North America	
PH	676	North America	
F	237	North America	
GH	72	North America	
MICH	72	North America	
CAS	63	North America	
A	47	North America	
LL	38	North America	
RSA	26	North America	
UC	13	North America	
DAV	5	North America	
TEX	3	North America	
	291,289		291,289

Now, through the API, innovation in plant taxonomy in Africa has been given a major boost with access to significant resources undreamed of in the past and impossible to visualize before now. Building on such a strong foundation, African plant scientists now have an opportunity not only to benefit from the advantages of global scientific integration, but indeed to be equal partners in providing access to previously untapped environmental resources for their own benefit. As with all the admirable principles underscoring NEPAD as a rapidly emerging peer review process for African states, it is also imperative that African taxonomists collaborate on the API, in equal partnership with their northern colleagues.

Multilateral cooperation on botanical matters is now possible at both a regional and global scale. In this regard, as government budgets constrict as a result of social demands, private and corporate investment in biodiversity science becomes increasingly important. Additional initiatives aimed at further improving conditions conducive to joint South-South and South-North scientific cooperation must be encouraged and supported at all levels. To achieve this, commitment to human resources development is of paramount importance. Indeed, human capital development was one of the primary aims of the Southern African Botanical Diversity

Network (SABONET) project, in many ways a forerunner of the API, which trained a cohort of over 200 African taxonomists and plant specialists (Steenkamp et al., 2006). Human capital improvement can therefore be achieved through placing education and training high on the projected development agenda. The API also contributes to promoting education and training in appropriate taxonomic methodologies, such as creating country-level checklists (Figueiredo & Smith, 2008) and e-technology used in creating images, databasing of associated metadata, and assisting in acquiring electronic infrastructure that will strengthen Africa's ability to participate in the API and to achieve its goals.

Strong regional networks of botanists, such as the one established through SABONET for southern and south-tropical Africa, have the potential to make immensely valuable contributions toward integrating the API with their day-to-day activities (Huntley et al., 2006). With this network in place, it now stands to reason that it should be expanded to the rest of Africa and be put to the test to deliver independently on further taxonomic outputs, beyond the scope of current project activities that include the imaging of specimens, literature, and artwork. With SABONET having been finalized and its output delivery consolidated, it has generated immense volumes of visible and tangible high-quality products (Klopper et al., 2006). With communication barriers now effectively abolished in the region, cross-border taxonomic activities are leading to the inevitable strengthening of electronic infrastructural development and concomitant improvement in technological proficiency. This will in turn lead to the achievement of even greater progress in human resources development. In this regard, the recent involvement in the API of the two southern African Lusophone countries, Angola and Mozambique is beginning to bear fruit with participating herbaria in these countries generating web-based content relating to their herbarium holdings, and joint South-South training courses in herbarium practice being planned.

A further imperative for Africa is the halting of environmental destruction, and this is where taxonomists and other biodiversity scientists can play a significant role. Only through the dissemination of useful information can the socio- and bio-importance of ecological services be emphasized, and this can only be achieved through integrated planning that addresses the basic needs for human well-being. The bioregional programs established for South Africa's Fynbos Biome—Cape Action for People and the Environment (CAPE) and the South African National Biodiversity Institute's Grassland Programme—are two excellent examples of environmental initiatives that use, among others, primary scientific information, including taxonomic data, in planning activities (Cadman et al., 2010: 145–151). Implementing change often takes time and involves risks. Our responsibility as taxonomists is to embrace the opportunities on offer, but we should not look elsewhere for leadership. Africa must take responsibility for its own future. On this road of development we must, simultaneously, accept the environmental and technological challenges that will be encountered and resolve them proficiently. The idea to digitize and disseminate herbarium specimen images electronically is by no means a new one. However, never before has this task been approached on such a massive scale and never has an indispensable environmental resource come into being in such a short amount of time. Appropriately, the focus of this global thrust has been initiated with the plants of Africa, a continent that is in the process of reinventing itself, among other things through having widely adopted the NEPAD (Klopper et al., 2002).

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EMBRYOLOGICAL EVIDENCE SUPPORTS THE TRANSFER OF *LEITNERIA FLORIDANA* TO THE FAMILY SIMAROUBACEAE[1]

Hiroshi Tobe[2]

ABSTRACT

Leitneria floridana Chapm., a shrub indigenous to North America, was long considered to be the sole member of the family Leitneriaceae, with uncertain affinities in and outside the class Amentiferae. Recent molecular analyses, however, show that the species is closely related to the genera *Brucea* J. F. Mill., *Soulamea* Lam., and *Amaroria* A. Gray in the family Simaroubaceae. Here, I report embryological features of *L. floridana* and provide anatomical corroboration for the molecular simaroubacean affinities of this species. I compared its embryology with those of the families Simaroubaceae, Meliaceae, and Rutaceae, which form a monophyletic clade in the order Sapindales. Comparisons showed that although *Leitneria* Chapm. resembled all three families embryologically, it fits best within the Simaroubaceae through possession of an unspecialized chalaza, straight and exarillate seeds, a non-multiplicative testa, a non-crystalliferous endotesta, and absence of a fibrous exotegmen. Within the Simaroubaceae, *Leitneria* also shares with *Brucea* the synapomorphies of a micropyle formed by an elongate, irregularly folded inner integument and a persistent tegmen composed only of endotegmen. Members of the Simaroubaceae are still poorly known embryologically, but available evidence supports the close affinity of *Leitneria* and *Brucea*.

Key words: *Brucea*, embryology, *Leitneria*, Sapindales, seed structure, Simaroubaceae.

Leitneria floridana Chapm. (Florida corkwood) is a dioecious shrub found in low, wet areas of the southeastern and south-central United States and is the only species of the genus with characteristic erect catkins (Channell & Wood, 1962; Bogle, 1997). The genus was first placed in the family Myricaceae (Chapman, 1860: 427), and thereafter, because of its uncertain affinities, was reassigned to become the sole member of the family Leitneriaceae, placed variously within the orders in and outside of the class Amentiferae: Leitneriales (e.g., Bentham & Hooker, 1880; Hjelmquist, 1948; Channell & Wood, 1962; Melchior, 1964; Cronquist, 1981; Bogle, 1997), Sapindales (Dahlgren, 1980), Rutales (including Sapindales) (Thorne, 1992), or Leitneriales near Sapindales (Takhtajan, 1997), or the superorder Rutanae (Takhtajan, 2009). Affinities with the family Simaroubaceae were first suggested by serological studies (Petersen & Fairbrothers, 1983, 1985). Petersen and Fairbrothers (1983) obtained antigens from *Leitneria* Chapm. pollen protein extracts and found that the strongest reactivity of *Leitneria* antigen was with *Ailanthus* Desf. and *Picrasma* Blume, both genera in the Simaroubaceae. Thereafter, molecular analyses based on *rbcL* sequences (Chase et al., 1993; Fernando et al., 1995; Gadek et al., 1996) consistently showed that *Leitneria* is best positioned in the Simaroubaceae, a family forming a clade inclusive of the families Rutaceae and Meliaceae in the order Sapindales. The Angiosperm Phylogeny Group (1998, 2003, 2009) accepted *Leitneria* as a member of the Simaroubaceae (see also Thorne & Reveal, 2007).

Most recent molecular analyses based on sequences from three plastid genes (*rbcL*, *atpB*, and *matK*) and a nuclear gene (*phyC*) show that *Leitneria* is sister to a clade comprising the genera *Brucea* J. F. Mill., *Soulamea* Lam., and *Amaroria* A. Gray within the Simaroubaceae (Clayton et al., 2007). This is a striking result and an example of the way in which molecular analyses have successfully resolved long-standing systematic uncertainties. Our concern was to find morphological synapomorphies likely to corroborate the sister-group relationship between *Leitneria* and the clade comprising *Brucea*, *Soulamea*, and *Amaroria*. Clayton et al. (2007: 1334) opined that morphological synapomorphies for these genera "may be difficult to detect due to the dramatic floral divergence of *Leitneria*."

I have long been interested in the relationships of *Leitneria* and have studied the genus embryologically for comparison with purportedly related taxa. More than 50 embryological characters are relevant to the development of the anther, ovule, and seed,

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which have often provided evidence of relationships among taxa ranging from species to families (Tobe, 1989). About 100 years ago, some of the embryological characters of *Leitneria* were described by Pfeiffer (1912) for comparison with members of the Amentiferae; plants used for this study were cultivated at the Missouri Botanical Garden (MO). However, most of the characters were not documented with the precision expected in modern works, and many other aspects of embryology are as yet undescribed. We now need exact information on the largest suite of embryological characters for critical comparison with other members of the Simaroubaceae. In this study, I confirm or correct Pfeiffer's (1912) interpretations and document almost all of the embryological features of *L. floridana*. These are compared with characters of members of the Simaroubaceae, Meliaceae, and Rutaceae. I show the embryological relatedness of *Leitneria* within the Simaroubaceae, particularly with the genus *Brucea* and its relatives.

Materials and Methods

Staminate flower buds of *Leitneria floridana* at various stages of development were collected from trees cultivated at the Missouri Botanical Garden in 2000, 2001, and 2007 (voucher: U.S.A., Missouri, St. Louis City, Missouri Botanical Garden, cultivated, perhaps originated in Butler Co., MO, *W. G. D'Arcy 3653* [MO 2426777]), and pistillate flower buds and fruits at various stages of development from trees in Butler County, Missouri, in 2000 and 2001 (voucher: U.S.A., Missouri, Butler Co., edge of swamp, S side of Neelyville Jct., *W. G. D'Arcy et al. 4557* [MO 2155947]). Samples were fixed in five parts stock formalin/five parts glacial acetic acid/90 parts 50% ethanol (FAA). Flower buds and seeds were dehydrated through an ethanol series and then embedded in Technovit 7100 (Kulzer, Wehrheim, Germany) for microtoming. Serial resin sections cut at a thickness of 5–7 μm were stained with Heidenhain's hematoxylin and mounted in Entellan (Merck, Darmstadt, Germany). The slides' permanent mounts are housed at the Department of Botany of Kyoto University.

Results

Anthers and Microspores

The staminate inflorescence is composed of about 40 to 50 flowers (or partial inflorescences) that are spirally arranged on the fertile axis (Fig. 1A). Each staminate flower, which we interpret as a 3-flowered cymule (Abbe & Earle, 1940; Abbe, 1974), bears about 10 stamens and is subtended by the primary bract (Fig. 1B). The anther is tetrasporangiate (Fig. 1B, F). Prior to maturation the anther wall comprises five or six cell layers, namely an epidermis, an endothecium, two or three middle layers, and a tapetum (Fig. 1C). The anther epidermis is persistent but collapsed in places. How the middle layers form remains uncertain. The tapetum is glandular (Fig. 1D, E) and its cells are usually multinucleate, with three to five nuclei each (Fig. 1E). Nuclei in tapetal cells often appear to be fused. During maturation, the middle layers degenerate and the epidermal cells become somewhat enlarged. Cells of the endothecium become enlarged and develop fibrous thickenings (Fig. 1D, F, G). Anther dehiscence takes place along longitudinal slits, with each slit common to two thecal microsporangia (Fig. 1G).

In the absence of suitable study materials, I was unable to ascertain whether microspore mother cell meiosis is accompanied by simultaneous or successive cytokinesis. Microspore tetrads are predominantly tetrahedral (Fig. 1D). Mature pollen grains are 2-celled (Fig. 1H).

Megagametophyte and Nucellus

The pistillate inflorescence is composed of 12 to 15 flowers arranged spirally on the fertile axis (Fig. 2A). Each flower has a single pistil with an elongate style and a superior ovary, bearing a fertile ovule on the upper side and a rudimentary ovule on the lower side in an ovarian locule (Fig. 2B). The fertile ovule is epitropous with a micropyle pointing upward; it is crassinucellate. In the absence of the youngest flower buds, I was unable to determine the number of archesporial cells. Each of the youngest buds available (collected 4 March 2000) had a single megasporocyte differentiated beneath a parietal tissue that was two cell layers in thickness (Fig. 2C). The parietal cells further divide periclinally, resulting in a thick parietal tissue (more than 10 cells thick) by the time the female gametophyte develops (Fig. 2F). The megasporocyte undergoes meiosis, resulting successively in a dyad (Fig. 2D), and then a linear tetrad of megaspores (Fig. 2E), as reported by Pfeiffer (1912). In the megaspore tetrad, the chalazal megaspore is functional and the three micropylar megaspores degenerate (Fig. 2E, F). The functional megaspore develops sequentially into a 2- (Fig. 2G), 4- (Fig. 2H), and 8-nucleate female gametophyte (Fig. 2I), as reported by Pfeiffer (1912). Therefore, the mode of female gametophyte development corresponds to the Polygonum type (for diverse modes of female gametophyte development in

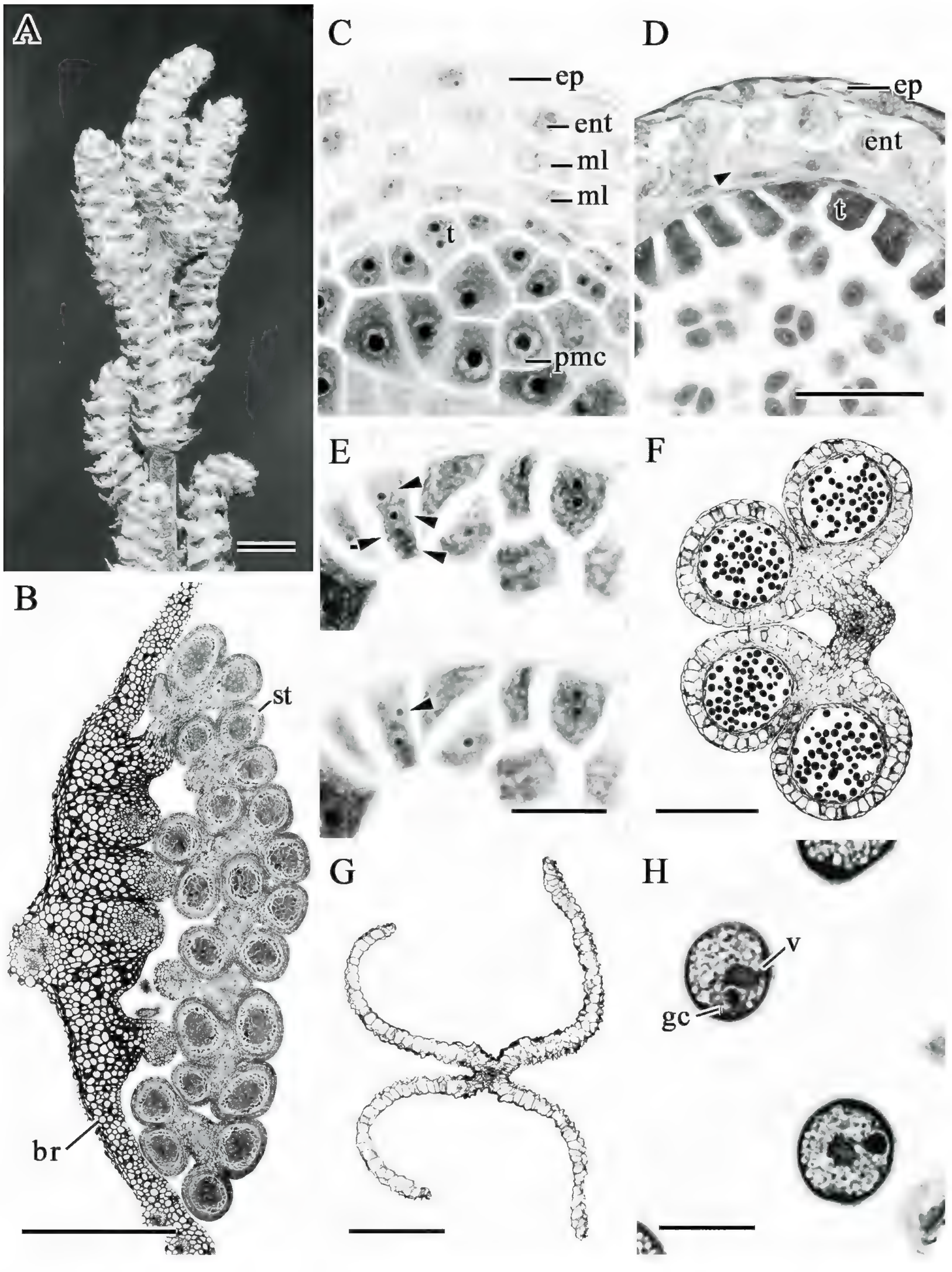

Figure 1. *Leitneria floridana*, development of anthers and microspores. —A. Staminate inflorescence. —B. Transverse section of a staminate flower (or partial inflorescence). —C. Transverse section of a young anther. —D. Transverse section of an older anther, showing a developing anther wall. Arrowhead indicates the degenerating middle layers. —E. Transverse section of an older anther, showing multinucleate glandular tapetal cells at two focal planes. Five nuclei in a single cell are indicated by arrowheads. —F. Transverse section of a nearly mature anther. —G. A mature anther dehisced along longitudinal slits. —H. Mature pollen. Abbreviations: br, bract; ent, endothecium; ep, epidermis; gc, generative cell; ml, middle layer; pmc, microspore mother cell; st, stamen; t, tapetal cell; v, nucleus of a vegetative pollen cell. Scale bars: A = 1 cm; B = 500 μm; F, G = 300 μm; D = 50 μm; C, E, H = 20 μm. A–H taken from *W. G. D'Arcy 3653* (MO).

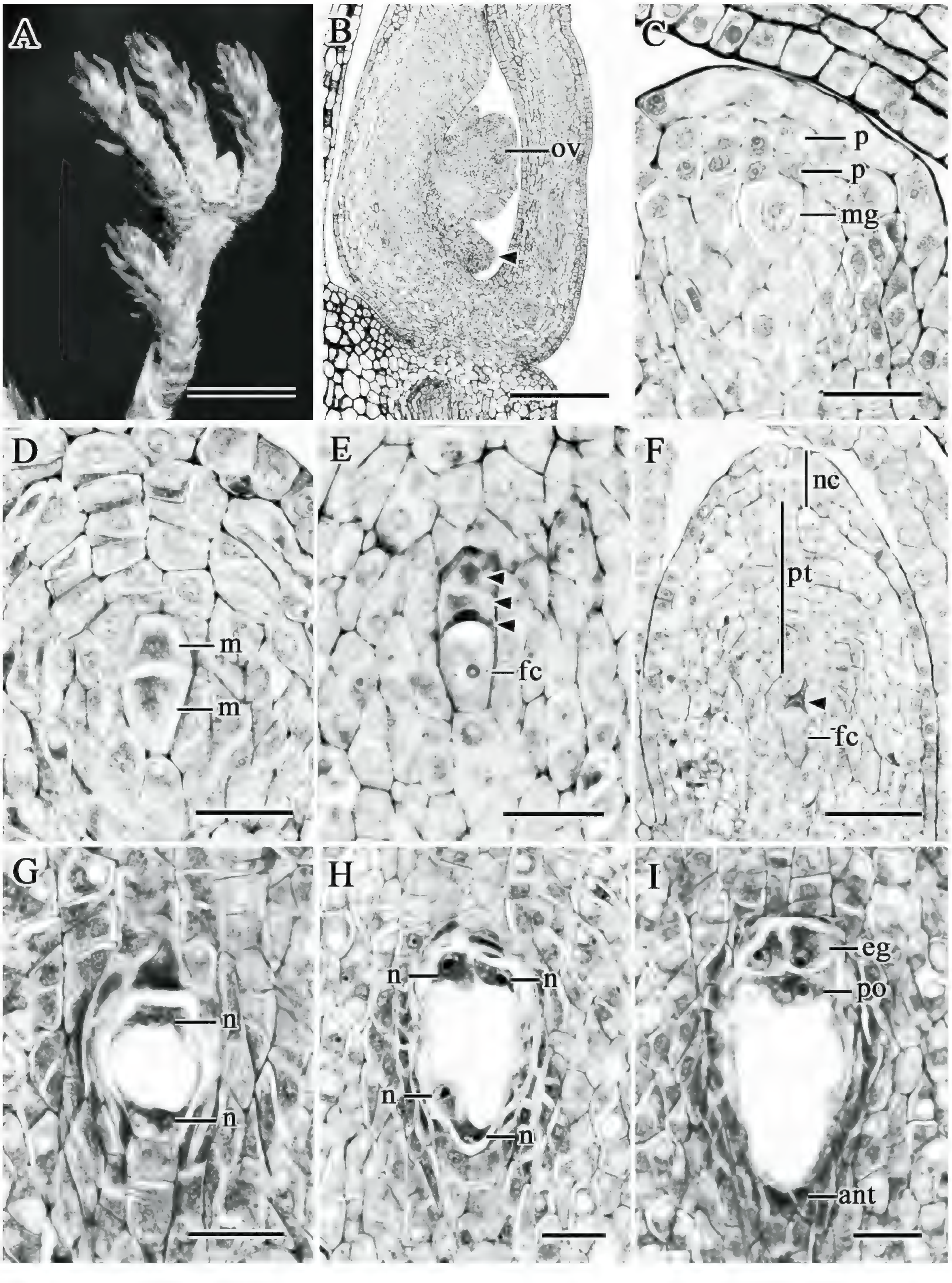

Figure 2. *Leitneria floridana*, development of ovules and female gametophytes. —A. Pistillate inflorescence. —B. Longitudinal section of a young pistil, showing one fertile ovule above and a lower rudimentary ovule (to left of arrowhead) in the locule. C–I. Longitudinal section of ovules in various stages of development. —C. Young ovule with a megasporocyte. —D. Ovule with a dyad of megaspores. Each cell is at meiotic metaphase II, with the chromatids equatorially aligned. —E. Ovule with a tetrad of megaspores; the upper three spores (to left of arrowheads) are degenerating. —F. Ovule with a uninucleate female gametophyte. Note a thick nucellar cap and thick parietal tissue have formed. —G. Binucleate female gametophyte or embryo sac. —H. Four-nucleate stage of the female gametophyte visualized by combining four consecutive serial sections. —I. Mature female gametophyte, visualized by combining two consecutive serial sections. One cell of an egg apparatus appears in the following section. Abbreviations: ant, antipodal cell; eg, egg cell; fc, functioning megaspore; m, megaspore; mg, megasporocyte; n, nucleus of female gametophyte; nc, nucellar cap; ov, ovule; p, parietal cell; po, polar nuclei; pt, parietal tissue. Scale bars: A = 1 cm; B = 200 μm; F, I = 50 μm; C–E, G, H = 20 μm. A–I taken from *D'Arcy, Porter & Demeree 4557* (MO).

angiosperms, see Stuessy, 2009: 216). The organized mature female gametophyte is ellipsoidal, comprising an egg cell, two synergids, two polar nuclei, and three antipodal cells. The three antipodal cells are ephemeral (Fig. 2I) and disappear soon after fertilization. During megasporogenesis, the apical dermal cells of the nucellus divide periclinally to form a nucellar cap that is three cell layers thick (Fig. 2F), as reported by Pfeiffer (1912).

At maturity, the ovule is hemitropous with the micropyle oriented at right angles to the chalaza (Fig. 3D). The nucellar tissue is very thick around the mature female gametophyte (Fig. 3D). At this stage, the parietal tissue lying above the mature female gametophyte is up to 15 cell layers thick (Fig. 3D). It thickens further and persists through post-fertilization stages without being crushed by the enlarging female gametophyte (Fig. 4A, D, E); it may also persist in mature seeds. No set sequence of further development occurs in the chalaza, which may result, for example, in pachychalazy. A hypostase does not differentiate, even in post-fertilization stages. No conspicuous obturator is formed.

INTEGUMENTS

The ovule is bitegmic (Fig. 3A–D). The inner integument is initiated first and the outer integument much later and is always shorter than the inner (Fig. 3A–C). On the antiraphal side, both the inner and outer integuments are initially two cells thick (Fig. 3A), but through anticlinal divisions of inner epidermal cells, soon become three cells thick along most of their lengths (Fig. 3B–E). In contrast, on the raphal side, the inner integument is thicker, dividing to four cells thick (Fig. 3B). Neither the inner nor the outer integument is multiplicative, so that their respective thicknesses do not change throughout development. No vascular supply was found in either the inner or outer integument.

The micropyle is formed by the inner integument alone when the female gametophyte is in the early 2- to 4-nucleate stage. This integument grows beyond the apex of the nucellus within the confined space of the locule, so that its tip is extremely elongated and irregularly folded (Fig. 3D).

ENDOSPERM AND EMBRYO

Although I did not confirm pollen tube passage through the micropyle, there is no doubt that the pollen tube grows from the nucellar apex to the female gametophyte through the thick parietal tissue (Fig. 4A). In post-fertilization stages, cell divisions continue in the nucellus, so that a thick nucellar tissue is formed on the chalazal side (Fig. 4B). A circumscribed nucellar tissue eventually disappears as the seed grows, but a degenerating fragment may remain in mature seeds (Fig. 4I).

Endosperm formation is of the nuclear type, and free nuclei are observed in the female gametophyte during early embryogenesis (Fig. 4C), as reported by Pfeiffer (1912). By the early stages of embryogenesis, the endosperm is cellularized centripetally (Fig. 4D). In mature seeds, the 10- to 30-cell-layered endosperm remains located outside the large embryo (Fig. 4H).

I did not examine embryogenesis in detail in this study, but fragmentary data on early and later embryogenesis indicate that the process progresses normally from proembryos through fully developed embryos (Fig. 4C–E). The suspensor is not especially large (Fig. 4E). The embryo in a mature seed is straight, large, and dicotyledonous (Fig. 4F).

SEED AND SEED COAT

Fruits are straight drupes with smooth surfaces that are about 27–30 mm long and 5–8 mm wide, each containing a single seed (Fig. 4F, upper right). The seed is enclosed by a hard endocarp composed of sclerotic cells (Fig. 4F). When the seed is still young, the coat comprises a 3- or 4-cell-layered tegmen (i.e., a developed inner integument) and a 4- or 5-cell-layered testa (i.e., a developed outer integument) (Fig. 4G). Among cells of the tegmen, those of the innermost layer, that is, the endotegmen, stain darkly, while cells of the outer layers are not specialized (Fig. 4G). Within the layers of the testa, the outermost layer cells are somewhat enlarged, while those of the other layers are unspecialized (Fig. 4G).

Mature seeds are straight and exarillate. The testa is slightly multiplicative and becomes five to 11 cell layers thick (Fig. 4H, I). Although most of the cell layers of the testa persist, those of the tegmen degenerate (except for the innermost layer). Thus, the mature seed coat comprises a 5- to 11-cell-layered testa and a 1-cell-layered tegmen (i.e., an endotegmen) (Fig. 4I). Cells of the exotesta are variously enlarged and contain scattered granular pigments. Cells of the mesotesta and endotesta are unspecialized, although Pfeiffer (1912: 198) observed pitted walls in all of them. Cells of the endotegmen have slightly thickened walls, as observed by Pfeiffer (1912). The seed coat may be categorized as testal (for seed coat terminology, see Corner, 1976; Schmid, 1986).

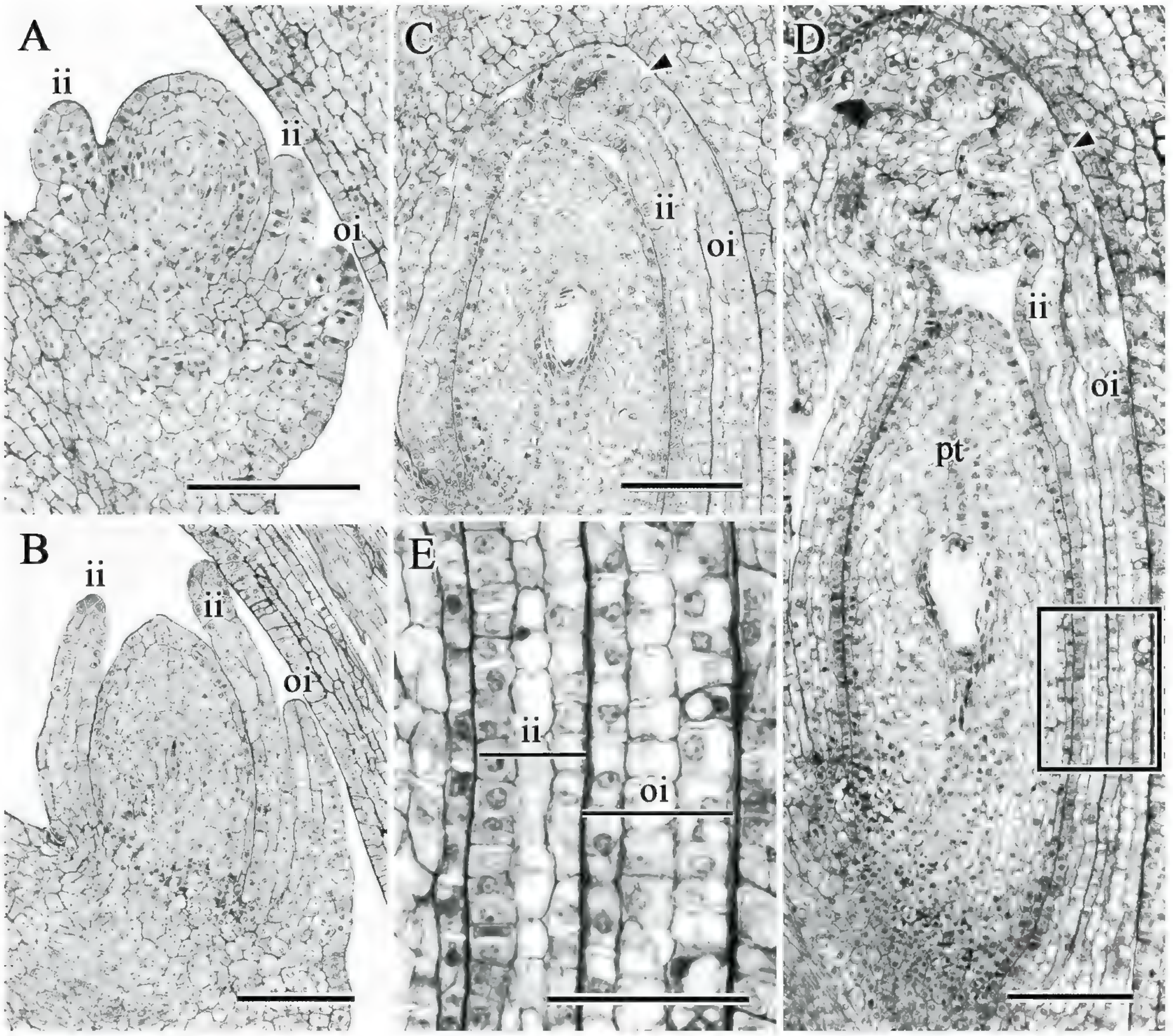

Figure 3. *Leitneria floridana*, development of integuments and micropyle. —A–D. Longitudinal sections of young and mature ovules showing development of the integuments as the ovules develop in the sequence from A to D. All sections were cut through the raphe to the antiraphe. Note that the outer integument is always shorter than the inner and that the micropyle is formed by the inner integument alone, which develops beyond the nucellar apex and becomes irregularly folded in an ovarian locule (D). Arrowheads in C and D indicate the position of the tip of the outer integument. —E. Magnified view of the ovule enclosed by a rectangle in D. Abbreviations: ii, inner integument; oi, outer integument; pt, parietal tissue. Scale bars: A–D = 100 μm; E = 50 μm. A–E taken from *D'Arcy, Porter & Demeree 4557* (MO).

Discussion

Summary of Embryological Features

Prior to my analysis, information on the development of the anther, ovule, and seed was fragmentary, although a few embryological characters were described by Pfeiffer (1912). My work provides most of the missing information and updates current concepts for several characters. Here, I summarize what is now known about the embryology of *Leitneria floridana* (see also Table 1).

The anther in *Leitneria floridana* is tetrasporangiate, with the anther wall five or six cell layers thick and of uncertain formation. The anther epidermis is persistent but partially collapsed; the endothecium is fibrous; two or three middle layers are crushed; the tapetum is glandular, its cells usually multinucleate and containing more than three nuclei. Cytokinesis in the microsporocyte is uncertain; microspore tetrads are predominantly tetrahedral, and pollen grains are 2-celled when shed.

The ovule in *Leitneria floridana* is hemitropous and crassinucellate, and the number of archesporial cells is uncertain, but the youngest ovules observed have a single megasporocyte beneath a 2-cell-layered parietal tissue, with the parietal tissue thickening to 15 cell layers by the mature female gametophyte stage. The megasporocyte undergoes meiosis, and the megaspore tetrads are linear. The chalazal megaspore is functional, developing into an 8-nucleate Polygonum-type female gametophyte, and the antipodal cells are ephemeral. Apical nucellar epidermal cells are periclinally divided, forming a 3-cell-layered

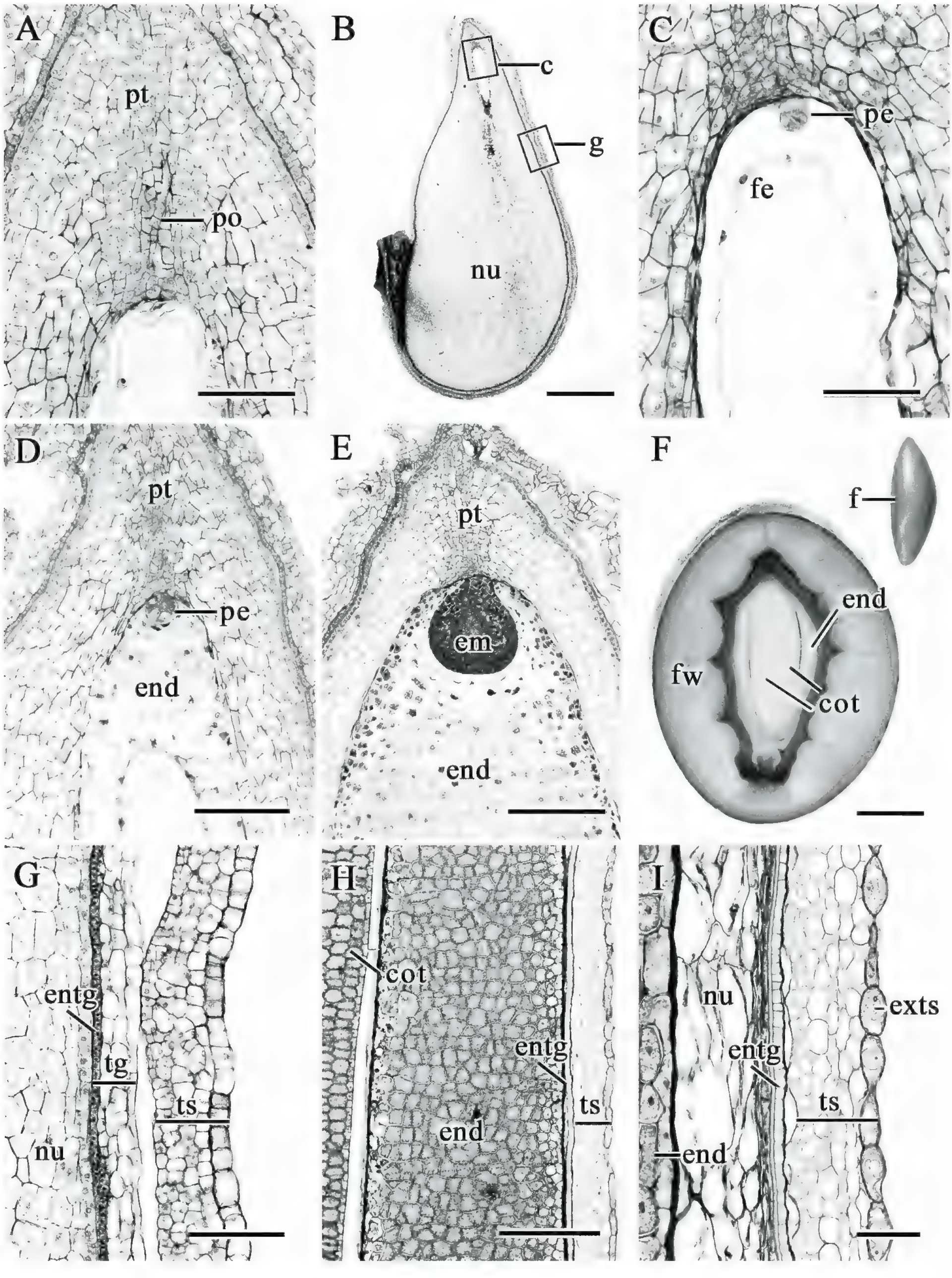

Figure 4. *Leitneria floridana*, development of seeds and seed coats. —A. Longitudinal section of a young seed. —B. Longitudinal section of an entire young seed, showing a thick nucellar tissue. —C. Magnified view of the young seed portion enclosed by rectangle to left of c in B, showing free endosperm nuclei. —D. Longitudinal section of a young seed showing a proembryo and a cellularized endosperm. —E. Longitudinal section of an embryo. —F. Transverse view of a mature fruit cut in upper and lower halves. Lateral view of the intact mature fruit shown at f in upper right. —G. Magnified view of the young seed enclosed by rectangle g in B, showing the structure of a young seed coat. —H. Part of a mature seed transverse section. —I. Part of a mature seed in longitudinal section. Abbreviations: cot, cotyledon; em, embryo; end, endosperm; entg, endotegmen; exts, exotesta; f, fruit; fe, free endosperm nucleus; fw, fruit wall; nu, nucellus; pe, proembryo; po, pollen tube; pt, parietal tissue; tg, tegmen; ts, testa. Scale bars: F = 2 mm; B = 1 mm; D, E, H = 200 μm; A, C, G = 100 μm; I = 50 μm. A–I taken from *D'Arcy, Porter & Demeree 4557* (MO).

Table 1. Comparisons in embryological characters among *Leitneria* Chapm., Simaroubaceae (except for *Leitneria*), Meliaceae, Rutaceae, and Sapindaceae. Data of the Simaroubaceae (except for *Leitneria*), Meliaceae, Rutaceae, and Sapindaceae are based on six, 18, 35, and 20 genera, respectively, whose embryological information is available (see text for all generic names).

	Leitneria	Simaroubaceae	Meliaceae[4]	Rutaceae[9]	Sapindaceae
Anthers and microspores					
Number of sporangia	4	4	4	4	4
Oil gland in anther tissue	absent	absent	absent	scattered	absent
Anther wall formation	?	?	?	?	?
Thickness of anther wall	5 to 6 cells thick	5 to 6 cells thick	5 to 6 cells thick	6 to 7 cells thick	4 to 5 cells thick
Anther epidermis	persistent	persistent	persistent, often papillate	flattened	persistent, flattened
Endothecium	fibrous	fibrous	fibrous	fibrous	fibrous
Middle layers	2 to 3 cells thick, crushed	3 to 4 cells thick, crushed	3 to 4 cells thick, crushed	3 to 4 cells thick, crushed	1 to 2 cells thick
Tapetum	glandular	glandular	glandular	glandular	glandular
Number of nuclei in a tapetal cell	3 to 5; fusing to form polyploid mass	3, 4, 6 to 12; fusing to form polyploid mass	2 to 4(10); fusing to form polyploid mass	2, 3, 4; fusing to form polyploid mass	1, 2, 3; fusing to form polyploid mass
Cytokinesis in meiosis	?	simultaneous	simultaneous	simultaneous	simultaneous
Predominant arrangement of microspore tetrads	tetrahedral	tetrahedral	tetrahedral	tetrahedral, decussate	tetrahedral
Number of cells in a mature pollen	2	2	2, 3	2	2
Anther dehiscence	longitudinal slits*	longitudinal slits	longitudinal slits	longitudinal slits	longitudinal slits
Ovule, nucellus, and megagametophyte					
Ovule orientation	hemitropous	anatropous or hemitropous	anatropous	anatropous (campylotropous in *Cneorum* L.)	ana-, hemi-, campylo-, or amphitropous
Number of archesporial cells	?	2- to 4-celled	1- or multicelled[5]	2- to 5-celled	1(to 4)-celled
Nature of nucellus	crassinucellate	crassinucellate	crassinucellate	crassinucellate	crassinucellate
Thickness of parietal tissue	10 to 15 cells thick	6 to 7 cells thick	6 to 8 cells thick	2 to 4 cells thick	4 to 15 cells thick
Shape of megagaspore tetrad	linear*	linear	linear	linear	linear
Mode of female gametophyte formation	Polygonum type	Polygonum type	Polygonum type	Polygonum type	Polygonum type
Shape of mature female gametophyte	ellipsoidal	obovoid	obovoid	ellipsoidal	narrowly ellipsoidal to lanceoloidal; somewhat curved
Antipodal cells	ephemeral	ephemeral	ephemeral	ephemeral	ephemeral (except in *Cardiospermum* L.)[13]
Nucellar cap	formed, 3-cell-layered	?	formed, 3- to 5-cell-layered or 7- to 9-cell-layered	formed	occasionally formed, 8- to 10-cell-layered (*Acer* L.)
Nucellar tissue in mature ovule	thick	thick	thick	thick	thick or lacking[14]
Specialization of chalaza	unspecialized	unspecialized (*Brucea* J. F. Mill., *Picrasma* Blume) or pachychalazal (*Quassia* L.)	usually pachychalazal[6]	unspecialized (rarely pachychalazal)[10]	enlarged to unspecialized[15]
Hypostase in ovule or young seed	not formed	formed	formed	formed	formed
Obturator	unspecialized	?	formed	funicular, hairy	funicular

Table 1. Continued.

	Leitneria	Simaroubaceae	Meliaceae[4]	Rutaceae[9]	Sapindaceae
Integuments					
Number of integuments	2*	2	2	2	2
Thickness of ii (early stage)	2 cells thick	?	2 cells thick	3 to 4 cells thick	?
Thickness of ii (late stage)	3 to 4 cells thick	2 to 6 cells thick	2 to 4 cells thick	3 to 4 cells thick	4 to 8 cells thick
Inner integument multiplicative?	no	no	no	no	slightly yes
Thickness of oi (early stage)	2 cells thick	?	2 cells thick	4 to 5 cells thick	?
Thickness of oi (late stage)	3 cells thick	3 to 10 cells thick	2 to 4 cells thick	4 to 5 cells thick	8 to 70 cells thick
Outer integument multiplicative?	no	usually no	no	no	yes
Vascular bundles in ii (or tegmen)	absent	absent	absent	absent	absent
Vascular bundles in oi (or testa)	absent	absent	absent	absent	present
Micropyle formation	ii	ii	ii, rarely ii and oi[7]	ii and oi	ii, or ii and oi
Micropyle form	ii, extremely elongated; irregularly folded	ii, extremely elongated, irregularly folded (*Brucea*); unspecialized (*Quassia*)[1]	unspecialized	unspecialized	unspecialized
Endothelium	not formed	not formed	not formed	not formed	not formed
Fertilization, endosperm, and embryo					
Path of pollen tube	probably porogamous	porogamous	porogamous	porogamous	porogamous
Mode of endosperm formation	nuclear	nuclear	nuclear	nuclear	nuclear
Type of embryogeny	?	Onagrad (*Brucea amarissima* (Lour.) Mill.)	?	Asterad, Onagrad, Solanad[11]	Asterad
Suspensor	not pronounced	not pronounced	not pronounced	not pronounced	not pronounced
Mature seed					
Shape or curvature	straight	straight	straight, often large	straight (curved in *Cneorum*)	curved
Aril or arilloid	absent	absent	often present (sometimes as a wing)[8]	rarely present (*Eriostemon* Sm., *Pilocarpus* Vahl, etc.)	present
Endosperm in mature seed	present, 10 to 30 cells thick	present, 6 to 7 cells thick[2]	present (absent in *Trichilia* P. Browne)	present or absent[12]	absent
Perisperm	absent	present, 3 to 4 cells thick	absent	absent	absent
Shape of embryo in mature seed	straight	straight	straight	straight (curved in *Cneorum*)	curved
Mature seed coat					
Seed coat type	testal	testal[3]	usually testal	usually exotestal or mesotestal	exotestal
Testa multiplicative?	yes (but weakly)	yes (but weakly)	usually yes	usually yes	yes
Thickness of testa	5 to 11 cells thick	3 to 10 cells thick	2 to 40 cells thick	4 to 21 cells thick	8 to 70 cells thick

Table 1. Continued.

	Leitneria	Simaroubaceae	Meliaceae[4]	Rutaceae[9]	Sapindaceae
Cells of exotesta	more or less enlarged, containing granular pigments	unspecialized (*Quassia*) or tubular (*Picrasma*, *Simarouba* Aubl.); walls slightly lignified (*Brucea*)	unspecialized, cuboidal, or palisadal; thin- or thick-walled, pitted	radially elongate (thus palisadal) in groups or evenly, longitudinally elongate, or cuboidal; walls thin or thick (sometimes fibrous); sometimes mucilaginous	typically palisadal, sometimes stellate-prismatic or flattened, rarely hairy
Cells of mesotesta	unspecialized	unspecialized or aerenchymatous; idioblasts scattered (*Simarouba*)	unspecialized and thin-walled when present; often collapsing or crushed	thin- or thick-walled, sometimes differentiating into an outer and an inner layer; cells of outer layer sometimes containing brown contents, and those of inner layer sometimes crushed or persistent with a crystal	unspecialized, a thick tissue composed of a compact outer half and an aerenchymatous inner half
Cells of endotesta	unspecialized	unspecialized (*Brucea*, *Quassia*), slightly lignified on radial and inner walls (*Picrasma*), or cuboidal with lignified pitted thickenings (*Simarouba*)	unspecialized, small, with 1 or 2 crystals	unspecialized or crystalliferous	unspecialized
Tegmen multiplicative?	no	no	usually no	no	usually no
Thickness of tegmen	1 cell thick*	crushed (*Picrasma*) or 1 cell thick (*Brucea*)	usually 4 to 7 cells thick, rarely 30 cells thick (*Carapa guianensis* Aubl.)	NA	3 to 12 cells thick
Cells of exotegmen	crushed*	crushed	usually fibrous	crushed	usually unspecialized
Cells of mesotegmen	crushed*	crushed	usually crushed; outer layers rarely persisting as elongate sclerotic cells	crushed	unspecialized
Cells of endotegmen	slightly thickened; containing darkly staining contents early in development	usually crushed, but persistent in *Brucea amarissima* with cells filled with darkly staining contents	unspecialized, small	crushed, rarely persistent, tanniniferous	unspecialized

Table 1. Continued.

	Leitneria	Simaroubaceae	Meliaceae[4]	Rutaceae[9]	Sapindaceae
References	Pfeiffer (1912), this study	Corner (1976), Nair & Joseph (1957), Nair & Sukumaran (1960), Narayana (1957), Wiger (1935)	Boesewinkel (1981), Corner (1976), Garudamma (1956, 1957), Ghosh (1966a, 1966b), Nair (1958, 1959a, 1959b), Narayana (1958), Prakash et al. (1977), Wiger (1935)	Bacchi (1943), Banerji (1954), Boesewinkel (1977, 1978, 1984), Boesewinkel & Bouman (1978), Corner (1976), Desai (1962), Johri & Ahuja (1957), Mauritzon (1935, 1936), Narayana (1963)	Banerji & Chaudhuri (1944), Corner (1976), David (1938), Guérin (1901), Haskell & Postlethwait (1971), Khushalani (1963), List & Steward (1965), Mauritzon (1936), Nair & Joseph (1960), Netolitzky (1926), Tobe & Peng (1990), van der Pijl (1957)

Abbreviations: ii, inner integument; oi, outer integument; NA, not applicable.

* Data of Pfeiffer (1912) were confirmed.

[1] This character has been reported by Wiger (1935) from *Ailanthus altissima* (Mill.) Swingle, *A. glandulosa* Desf., *A. malabarica* DC., *Brucea amarissima*, *Quassia amara* L., *Samadera indica* Gaertn., *S. mekongensis* Engl.; by Nair and Joseph (1957) from *S. indica*; by Nair and Sukumaran (1960) from *B. amarissima*; by Narayana (1957) from *A. excelsa* Roxb.; by Corner (1976) from *B. javanica* (L.) Merr. and *Q. indica* (Gaertn.) Noot.

[2] Endosperm is lacking in mature seeds in *Picrasma*, 6 to 7 cells thick in *Brucea* (Corner, 1976).

[3] Although the testa is unspecialized, its cells are persistent except in *Brucea javanica*, where they also degenerate (Corner, 1976).

[4] Data for *Chisocheton* Blume are excluded because the genus is obviously at a derived position in Meliaceae phylogeny (Muellner et al., 2003) and exhibits distinct features such as the unitegmy and orthotropy of ovule and the vascularized integument.

[5] It is reported that the ovule archesporium is 1-celled but sometimes 2- to 3-celled in *Naregamia alata* Wight & Arn. (Nair, 1959a) and *Cipadessa baccifera* (Roth) Miq. (Narayana, 1958), while it is multicelled, for instance, 3- to 4-celled in *Sandoricum indicum* Cav. (Nair, 1958), 6- to 8-celled in *Azadirachta indica* A. Juss. (Nair & Kanta, 1961), or up to 11-celled in *Lansium domesticum* Corrêa (Prakash et al., 1977).

[6] Pachychalazal or perichalazal seeds occur in many genera of the Melioideae and Cedreloideae (*Aglaia* Lour., *Aphanamixis* Blume, *Carapa* Aubl., *Dysoxylum* Blume, *Lansium* Corrêa, *Swietenia* Jacq., and *Trichilia*); seeds with these enlarged chalazae are rare in the Melioideae (*Melia azedarach* L.) and Cedreloideae (*Cedrela toona* Rottler).

[7] The micropyle is formed by the inner integument in *Naregamia alata* (Nair, 1959a), *Melia azedarach* (Nair, 1959b), *Sandoricum indicum* (Nair, 1958), *Azadirachta indica* (Garudamma, 1957; Nair & Kanta, 1961), and *Cipadessa baccifera* (Narayana, 1958), but it is formed by both the inner and outer integuments in *Aphanamixis grandiflora* Blume (Wiger, 1935) and *Lansium domesticum* (Prakash et al., 1977).

[8] Arillate seeds occur in some genera (*Aglaia*, *Aphanamixis*, *Dysoxylum*, and *Lansium*) of the Melioideae; winged seeds occur in the Cedreloideae (*Cedrela* P. Browne and *Swietenia*). Seeds of some genera (*Guarea* F. Allam. ex L., *Melia* L., and *Trichilia*) of Melioideae do not have appendages.

[9] Data for *Glycosmis* cf. *arborea* (Roxb.) DC. are excluded because the genus is obviously at a derived position in Rutaceae phylogeny (Muellner et al., 2003) and exhibits distinct features such as the unitegmy of ovule and the vascularized integument (Boesewinkel & Bouman, 1978).

[10] According to Corner (1976), seeds have unspecialized chalaza in most genera (*Calodendrum* Thunb., *Chloroxylon* DC., *Dictamnus* L., *Pilocarpus*, *Ruta* L., and *Zanthoxylum* L.) but are clearly pachychalazal in *Atalantia monophylla* (L.) DC. The pachychalazal seeds also occur in *Glycosmis* cf. *arborea* (Boesewinkel & Bouman, 1978).

[11] The Asterad type is reported in *Ravenia spectabilis* (Lindl.) Engl., Onagrad type in *Ruta graveolens* L., and Solanad type in *Citrus trifoliata* L.

[12] According to Corner (1976), seeds are albuminous in *Dictamnus albus* L. and *Ruta graveolens* but are exalbuminous in *Atalantia monophylla* and *Pilocarpus racemosus* Vahl.

[13] In *Cardiospermum halicacabum* L. the antipodal cells are usually more than three and as many as 14 cells are observed. They may be multinucleate and persist even after fertilization up to the 3- or 4-celled proembryo stage and degenerate afterward (Nair & Joseph, 1960).

[14] In *Cardiospermum halicacabum* the nucellar tissue is consumed by an enlarging female gametophyte except at the apical part (Nair & Joseph, 1960).

[15] According to Corner (1976), the chalaza of seed is unspecialized in *Alectryon* Gaertn. and *Dodonaea* Mill., distinctly enlarged in *Guioa* Cav. and *Sapindus* L., elongate transversely in *Nephelium* L., or develops into an extensively pachychalazal structure in *Allophylus* L., *Cardiospermum*, *Cupania* L., *Harpullia* Roxb., and *Paullinia* L.

nucellar cap; the hypostase is not differentiated, and the obturator is absent.

The ovule is bitegmic, with both the inner and outer integuments initially two cell layers thick, soon thickening to three (or four) cell layers. The inner and outer integuments lack vascular bundles, and the outer integument is always shorter than the inner. The micropyle is formed by the inner integument alone; the inner integument is extremely elongate to beyond the apex of the nucellus, and is irregularly folded.

Fertilization is probably porogamous in *Leitneria floridana*, with nuclear-type endosperm formation. The mature seeds are albuminous, with a 10- to 30-cell-layered endosperm. Embryogenesis is uncertain, and the mature seed embryo is straight, large, and dicotyledonous.

The mature seed is straight and exarillate; the mature seed coat is testal, comprising a 5- to 11-cell-layered testa and a 1-cell-layered tegmen (endotegmen); the other cell layers of the tegmen are crushed. Cells of the exotesta are slightly enlarged, containing granular pigments; cells of the mesotesta and endotesta are unspecialized, while those of the endotegmen are slightly thick-walled.

COMPARISONS WITH OTHER SIMAROUBACEAE AND RELATED FAMILIES

I compared the embryological features of *Leitneria* with those from a wide range of members of the Simaroubaceae (19 genera), Meliaceae (50 genera), and Rutaceae (161 genera), using the family Sapindaceae s.l. (including Aceraceae and Hippocastanaceae) as an outgroup. None of these families have been subjected to comprehensive embryological examination, and even for species investigated thus far, data are as yet fragmentary. Embryological data for the Simaroubaceae have been collected from 12 species of the genera *Ailanthus*, *Brucea*, *Picrasma*, *Quassia* L., *Samadera* Gaertn., and *Simarouba* Aubl. (Wiger, 1935; Nair & Joseph, 1957; Narayana, 1957; Nair & Sukumaran, 1960; Corner, 1976); those for the Meliaceae are from 18 genera in two major clades representing the subfamilies Cedreloideae (*Carapa* Aubl., *Cedrela* P. Browne, *Chukrasia* A. Juss., *Khaya* A. Juss., and *Swietenia* Jacq.) and Melioideae (e.g., *Aglaia* Lour., *Aphanamixis* Blume, *Chisocheton* Blume, *Cipadessa* Blume, *Dysoxylum* Blume, *Guarea* F. Allam. ex L., *Lansium* Corrêa, *Melia* L., *Naregamia* Wight & Arn., *Sandoricum* Cav., *Trichilia* P. Browne, *Turraea* L., and *Walsura* Roxb.) (Wiger, 1935; Garudamma, 1956, 1957; Nair, 1958, 1959a, 1959b; Narayana, 1958; Nair & Kanta, 1961; Ghosh, 1966a, 1966b; Corner, 1976; Prakash et al., 1977; Boesewinkel, 1981) within the family phylogeny (Muellner et al., 2003); those for the Rutaceae are from 35 genera (*Adenandra* Willd., *Aegle* Corrêa, *Agathosma* Willd., *Atalantia* Corrêa, *Boenninghausenia* Rchb. ex Meisn., *Boronia* Sm., *Calodendrum* Thunb., *Chloroxylon* DC., *Choisya* Kunth, *Citropsis* (Engl.) Swingle & M. Kellerm., *Citrus* L., *Clausena* Burm. f., *Cneorum* L., *Coleonema* Bartl. & H. L. Wendl., *Dictamnus* L., *Dictyoloma* A. Juss., *Diosma* L., *Empleurum* Aiton, *Eriostemon* Sm., *Erythrochiton* Nees & Mart., *Flindersia* R. Brown, *Fortunella* Swingle, *Glycosmis* Corrêa, *Limonia* L., *Melicope* J. R. Forst. & G. Forst., *Murraya* Köenig ex L., *Phellodendron* Rupr., *Pilocarpus* Vahl, *Poncirus* Raf., *Ptelea* L., *Ruta* L., *Skimmia* Thunb., *Spathelia* L., *Triphasia* Lour., and *Zanthoxylum* L.) (Mauritzon, 1935, 1936; Bacchi, 1943; Banerji, 1954; Johri & Ahuja, 1957; Desai, 1962; Narayana, 1963; Corner, 1976; Boesewinkel, 1977, 1978, 1984; Boesewinkel & Bouman, 1978); those for the Sapindaceae are from 20 genera (*Acer* L., *Aesculus* L., *Alectryon* Gaertn., *Allophylus* L., *Cardiospermum* L., *Cupania* L., *Diplopeltis* Endl., *Dodonaea* Mill., *Guioa* Cav., *Harpullia* Roxb., *Koelreuteria* Laxm., *Litchi* Sonn., *Magonia* A. St.-Hil., *Nephelium* L., *Paullinia* L., *Pometia* J. R. Forst. & G. Forst., *Sapindus* L., *Trigonachras* Radlk., *Ungnadia* Endl., and *Xanthoceras* Bunge) (Guérin, 1901; Netolitzky, 1926; Mauritzon, 1936; David, 1938; Banerji & Chaudhuri, 1944; van der Pijl, 1957; Nair & Joseph, 1960; Khushalani, 1963; List & Steward, 1965; Haskell & Postlethwait, 1971; Corner, 1976; Tobe & Peng, 1990). The Rutaceae and Sapindaceae, which are embryologically relatively well studied, have diverse features, particularly in seed and seed coat characters (Table 1). Thus, I collected embryological data for the Rutaceae from *Cneorum* (Boesewinkel, 1984), which represents the basal lineage within the family phylogeny (Muellner et al., 2007); data for the Sapindaceae were collected from *Xanthoceras* of the Xanthoceroideae (Guérin, 1901; Corner, 1976), which likely represents the first lineage to diverge within the entire family (Harrington et al., 2005).

Comparisons show that *Leitneria* has many embryological features in common with the Simaroubaceae, Meliaceae, Rutaceae, and Sapindaceae. Even features that appeared distinctive to *Leitneria* and were expected to be of use in critical comparisons (e.g., multinucleate anther-tapetal cells, thick nucellar cap) occurred widely in all of the families compared. Such shared features do not provide evidence of affinities between *Leitneria* and any particular family or limited group of families. However, *Leitneria* either shared or

Table 2. Embryological comparisons among *Leitneria* Chapm., Simaroubaceae (excluding *Leitneria*), Meliaceae, and Rutaceae (*Cneorum* L.). Character-state polarities were determined using the Sapindaceae (*Xanthoceras* Bunge) as an outgroup. Plesiomorphy is scored 0, and apomorphy 1. Data of the Simaroubaceae (except for *Leitneria*) and Meliaceae are based on six and 18 genera, respectively, whose embryological information is available (see text for all generic names). The numbers (1 to 11) that precede the characters correspond to the numbers appearing on the phylogenetic diagram in Figure 5.

Character	*Leitneria*	Simaroubaceae	Meliaceae	Rutaceae (*Cneorum*)	Sapindaceae (*Xanthoceras*)
1. Specialization of chalaza	unspecialized (0)	unspecialized (0)	pachychalazal or perichalazal (1)	unspecialized (0)	unspecialized
2. Seed shape or curvature	straight (1)	straight (1)	straight (1)	campylotropous (0)	campylotropous
3. Appendage (aril or wing) on seed	absent (0)	absent (0)	present (1)	absent (0)	absent
4. Testa multiplicative	no (1)	no (1)	yes (0)	no (1)	yes
5. Vascular bundles in testa	absent (1)	absent (1)	absent (1)	absent (1)	present
6. Cells of mesotesta	unspecialized (1)	unspecialized (1)	unspecialized (1)	unspecialized (1)	thick-walled
7. Endotesta crystalliferous	no (0)	no (0)	yes (1)	no (0)	no
8. Tegmen multiplicative	no (1)	no (1)	no (1)	no (1)	yes
9. Exotegmen fibrous when present	no (0)	no (0)	yes (1)	no (0)	no
10. Tip of inner integument forming a micropyle	elongated, irregularly folded (1)	elongated, irregularly folded (*Brucea* J. F. Mill.) (1); unspecialized (*Quassia*) (0)	unspecialized (0)	unspecialized (0)	unspecialized
11. Mature tegmen composed only of endotegmen	yes (1)	yes (*Brucea amarissima* (Lour.) Merr.) (1); no (0)	no (0)	no (0)	no

did not share 11 mature ovule or seed structures with all or some of the families compared. The respective character states in *Leitneria* and the related families are summarized in Table 2, and the distribution of apomorphies in nine characters is mapped on the phylogenetic diagram in Figure 5.

Leitneria and the families Simaroubaceae, Meliaceae, and Rutaceae all have a non-vascularized testa, an unspecialized mesotesta, and a non-multiplicative tegmen (see characters 5, 6, and 8 in Table 2); the family Sapindaceae (*Xanthoceras*) has vascular bundles in the testa (which develops into a persistent tissue composed of thick-walled cells) and a multiplicative tegmen that develops into a thick, permanent tissue. These shared features are likely to be synapomorphies, corroborating known close molecular relationships among the Simaroubaceae, Meliaceae, and Rutaceae (Fernando et al., 1995; Gadek et al., 1996; Muellner et al., 2007). Among these families, the Meliaceae are characterized by pachychalazal or perichalazal seeds, arillate or winged seeds, a crystalliferous endotesta, and a fibrous exotegmen (characters 1, 3, 7, and 9). In contrast to the Meliaceae, which have family-specific characteristics, the Simaroubaceae and Rutaceae appear to have no autapomorphies. The Simaroubaceae have straight seeds in common with the Meliaceae (character 2) and a non-multiplicative

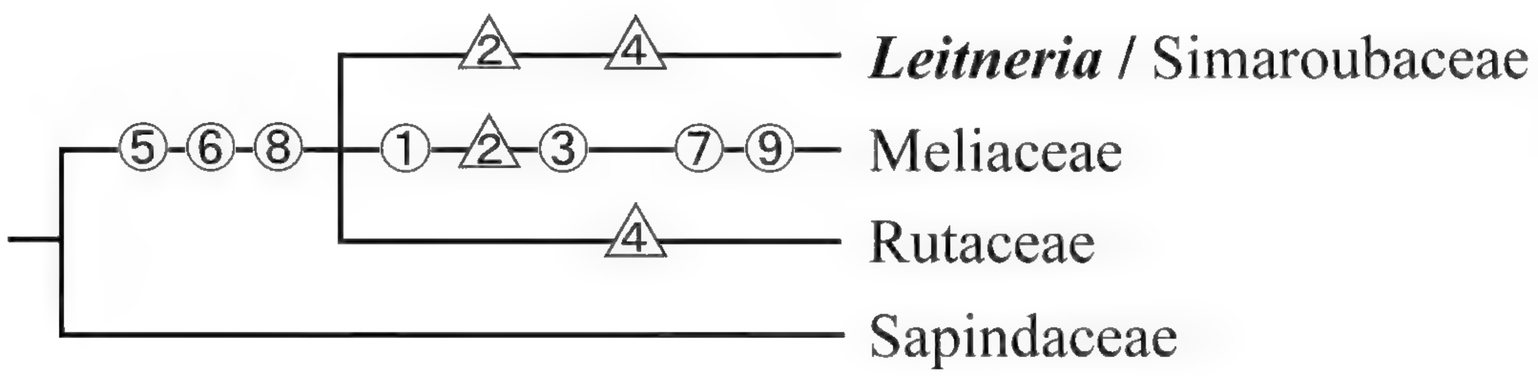

Figure 5. Phylogenetic diagram (modified from Muellner et al., 2007) for *Leitneria*, Simaroubaceae (excluding *Leitneria*), Meliaceae, Rutaceae, and Sapindaceae (outgroup), showing the distribution of apomorphies in Table 2. Numbers correspond to character states described in Table 2; a character enclosed in a circle indicates a synapomorphy or autapomorphy, while a triangle denotes a synapomorphy or homoplasy.

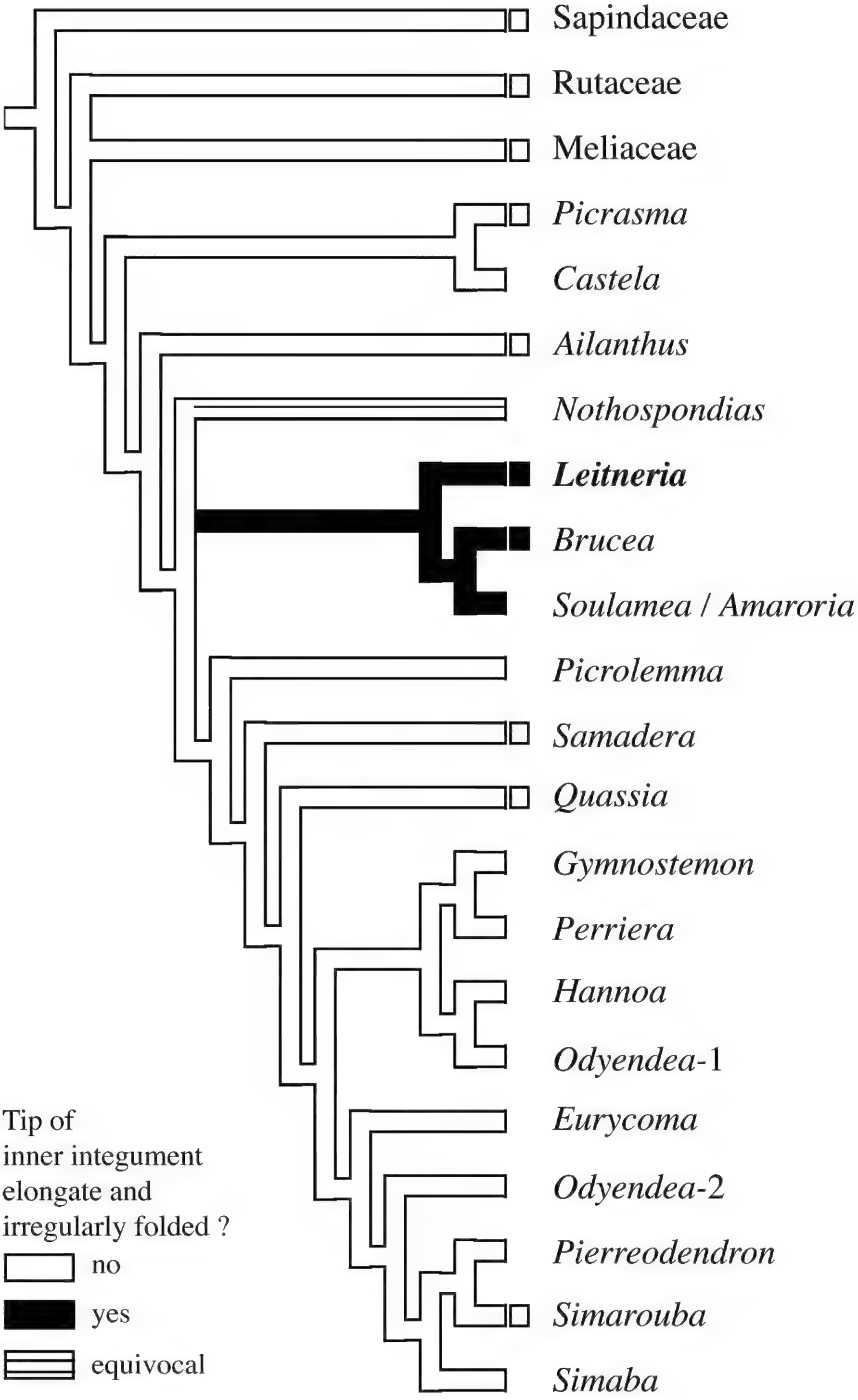

Figure 6. Taxonomic distribution of micropyles formed by elongated, irregularly folded inner integuments within the phylogenetic tree for the Simaroubaceae (modified from Clayton et al., 2007).

testa in common with the Rutaceae (character 4). All of these seed and seed coat features are found in *Leitneria*. Thus, although an understanding of simaroubaceous embryological features is still incomplete, *Leitneria* apparently fits best within the family Simaroubaceae.

COMPARISONS BETWEEN *LEITNERIA* AND OTHER SIMAROUBACEAE

Among simaroubaceous genera for which embryological data are available, *Brucea* has the closest resemblance to *Leitneria* in that both genera form a micropyle from an elongate, irregularly folded inner integument (see character 10 in Table 2). In addition to the two species of *Brucea*, micropyle formation has been examined in eight species of the genera *Ailanthus*, *Quassia*, and *Samadera* (see footnote 1 in Table 1). Wiger (1935: 83), who examined six species of *Ailanthus*, *Quassia*, and *Samadera* in addition to *B. amarissima* (Lour.) Merr., noted that "The further development in *Brucea* is rather interesting. The inner integument is tube-like and lengthened and by pushing against the placenta more or less folded, the micropyle thus being rather long and winding." Nair and Sukumaran (1960), who also studied ovule development in *B. amarissima*, did not examine the micropyle, but a drawing of the mature ovule (Nair & Sukumaran, 1960: 176, fig. 28) clearly demonstrates that the micropyle is formed by an elongate, irregularly folded inner integument. A similar micropyle structure is also found in *B. javanica* (L.) Merr. (Corner, 1976: 459, fig. 536); Corner (1976: 253) reported that in *B. javanica* the inner integument elongates beyond the exostome and is often splayed out against the carpel wall. As noted above, a molecular sister-group relationship exists between *Leitneria* and the clade comprising *Brucea*, *Soulamea*, and *Amaroria* (Clayton et al., 2007). When mapped on the phylogenetic tree of the Simaroubaceae with MacClade vers. 3.04 software (Maddison & Maddison, 2005), micropyles formed from an elongate, irregularly folded inner integument were restricted to *Leitneria* and the clade containing *Brucea*, *Soulamea*, and *Amaroria* (Fig. 6). Thus, a morphological synapomorphy very likely unites *Leitneria* and the clade comprising *Brucea*, *Soulamea*, and *Amaroria* (Fig. 6). We have no information on the micropyles of *Soulamea* and *Amaroria*, but they may share with *Leitneria* and *Brucea* a micropyle formed by an elongate, irregularly folded inner integument. The significance of this type of micropyle formation is not clear, but it may play a role in selecting pollen for fertilization, particularly in the anemophilous *Leitneria*.

Seed coat structure may provide yet another synapomorphy for the clade containing *Leitneria*, *Brucea*, *Soulamea*, and *Amaroria*. In *Leitneria* the mature seed coat is composed of a testa with five to 11 cell layers and a tegmen of just one cell layer (i.e., an endotegmen). While the cells of the testa are little specialized, those of the endotegmen, which is the only persistent cell layer in the tegmen (character 11 in Table 2), stained darkly early in development and were somewhat thick-walled at maturity. According to Nair and Sukumaran (1960), cells of the endotegmen in *B. amarissima* are persistent and have thick walls and a dense accumulation of darkly staining contents. Thus, the seed coat structure of *Leitneria* is very similar to that of *B. amarissima*. Corner (1976) reported that all cells of the tegmen are crushed in *B. javanica*, *Picrasma javanica* Blume, *Quassia indica* (Gaertn.) Noot., and *Simarouba* spp., but this needs confirmation because observations on *B. amarissima* (Nair & Sukumaran, 1960) and *B. javanica* (Corner, 1976) are not concordant.

Leitneria has a very thick parietal tissue in the nucellus that persists until late in the post-fertilization stages. In other angiosperms, the parietal tissue is generally destroyed by an enlarging female gametophyte before and after fertilization. The persistent thick parietal nucellar tissue of *Leitneria* may provide another key character for future comparisons with other Simaroubaceae.

In conclusion, although previous morphology-based systematic treatments have not suggested a simaroubaceous affinity for *Leitneria*, my embryological studies showed that features of the genus are concordant with members of the Simaroubaceae, particularly *Brucea*, corroborating molecular evidence (Clayton et al., 2007). Extensive studies on the Simaroubaceae (particularly genera considered basal [e.g., *Ailanthus*, *Castela* Turpin, and *Picrasma*] in the family phylogeny) would provide invaluable evidence for further assessment of the systematic position of *Leitneria*.

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Erratum

Ulloa U., C., D. L. Nickrent, C. Whitefoord & D. L. Kelly. 2010. *Hondurodendron*, a New Monotypic Genus of Aptandraceae from Honduras. Ann. Missouri Bot. Gard. 97: 457–467.

In Table 1, the incorrect GenBank numbers were printed for *Hondurodendron* and *Harmandia* in the *matK* and *accD* columns. The correct data can be found in the following revised table. The authors regret the error.

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Table 1. Voucher information and GenBank accession numbers for 10 taxa used in the phylogenetic analysis. The DNA accession numbers refer to the collections by D. L. Nickrent archived at Southern Illinois University Carbondale. Sequences in boldface were newly generated for this study. NHN, National Herbarium of the Netherlands.

Taxon	Voucher	Herbarium	Country	DNA accession number	SSU rDNA	*rbcL*	*matK*	*accD*
Anacolosa papuana Schellenb.	*Regalado & Sirikolo 692*	MO	Solomon Islands	4247	DQ790104	DQ790144	DQ790181	DQ790250
Aptandra tubicina (Poepp.) Benth. ex Miers	*van der Werff & Vasquez 13846*	MO	Peru	4202	DQ790105	DQ790141	DQ790178	DQ790247
Cathedra acuminata (Benth.) Miers	*Ratter et al. 6782*	MO	Brazil	4244	**FJ848847**	DQ790145	DQ790182	DQ790251
Chaunochiton kappleri (Sagot) Ducke	*Zamora 1928*	MO	Costa Rica	3052	DQ790106	DQ790142	DQ790179	DQ790248
Harmandia mekongensis Baill.	*Koizumi 1411*	KYO	Indonesia	5597	**FJ848849**	**FJ848842**	**FJ848846**	**FJ848844**
Hondurodendron urceolatum C. Ulloa, Nickrent, Whitef. & D. Kelly	*Fagan et al. DA/2/MS 313-II*	MO	Honduras	5555	**FJ848848**	**FJ848841**	**FJ848845**	**FJ848843**
Maburea trinervis Maas	*Zagt s.n.*	NHN	Guyana	4256	DQ790114	DQ790165	DQ790201	DQ790268
Ongokea gore (Hua) Pierre	*Breteler et al. 14888*	NHN	Gabon	4184	DQ790120	DQ790140	DQ790177	DQ790246
Phanerodiscus capuronii Malécot, G. E. Schatz & Bosser	*Schatz et al. 3439*	MO	Madagascar	4204	DQ790122	DQ790143	DQ790180	DQ790249
Strombosiopsis tetrandra Engl.	*Wieringa 3300*	NHN	Gabon	4055	DQ790125	DQ790155	DQ790191	DQ790259

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WHY ARE WE STILL PRODUCING PAPER FLORAS?[1]

Anthony R. Brach[2] *and David E. Boufford*[3]

Abstract

Advances in online resources and electronic publication provide the sciences with tools to revolutionize education and research (e.g., cataloging, data archiving and access, and identification). Older journals and monographs are being scanned and increasingly posted online quickly by book scanning projects, although even for new issues, there can be a "moving wall" or lag time (e.g., BioOne and JSTOR). Some scientific disciplines are providing the public with pre-print access to articles in digital libraries, while manuscript availability in other disciplines, such as nomenclatural botany, is often delayed until the time of print publication. Within botany, taxonomic treatments should be provided online at all stages of preparation and revision (in certain cases following initial editing). Now, many published floras can be browsed and searched online (e.g., Flora of North America, Jepson Manual, Flora of Australia). The Flora of China Project provides treatments at all stages, online, prior to printing of volumes. Because of this visibility, the Flora of China Web site regularly receives questions from the general public and helpful review comments from botanists worldwide. With pressing issues of cataloging biodiversity, conservation, and sustainable use of resources, botanists are challenged to prepare and revise online treatments, including interactive identification keys and images, for a worldwide audience of students and researchers.

Key words: digital floras, digital libraries, electronic publication, Flora of China, interactive identification keys, species-id.net.

With the pressing issues of conservation and naming and describing the world's species (Wheeler et al., 2004), electronic publishing (Lancaster, 1995) provides the tools to revolutionize education and research (e.g., cataloging, data archiving and access, and identification; also see Rosatti & Duncan, 1995). Today, older books, journals, and monographs are being scanned and posted quickly by Google Books

[1] We are thankful to numerous individuals for their discussions of this topic. We thank Flora of China Project contributors, editors, and reviewers for allowing their draft and revised treatments to be posted online. We are grateful to Hong Cui (University of Arizona) for using the Flora of China treatments as a test of the MARTT system and for providing the Greenstone Digital Library, Gregor Hagedorn (Julius Kühn-Institute, Germany) for creating the open data repository on species-id.net, Hong Song (St. Louis University) for incorporating floristic volumes into eFloras.org, Myriam Fica (MO) for assistance in updating the data, and Anne Marie Countie (Harvard University) and Chris Freeland (MO) for their support of servers at the Harvard University Herbaria and Missouri Botanical Garden, respectively. We are thankful for helpful comments by the editor Victoria Hollowell (MO) and three reviewers: Tom Rosatti (JEPS), Peter F. Stevens (MO), and Mike Dallwitz (Giralang, Australia). Support of the U.S. National Science Foundation (BSR-8906215, BSR-9201378, DEB 9626806, DEB 0072682, DEB 0343439, DEB-0514279, DEB-0722217, DEB-0810237, and DEB-0813935) for the Flora of China Project is gratefully acknowledged.

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(<http://books.google.com>), the Biodiversity Heritage Library (<http://www.biodiversitylibrary.org>), and the Botanicus Digital Library (<http://www.botanicus.org>). These projects are constructing extensive digital libraries (Greenstein & Thorin, 2002). Even for new issues, though, there can be a "moving wall" or lag time (e.g., BioOne: <http://www.bioone.org/> and JSTOR: <http://www.jstor.org/>).

Now, several scientific disciplines (e.g., medicine, astronomy, chemistry, and physics) are providing the public with pre-print access to articles (Tomaiuolo & Packer, 2000). Online, peer-reviewed, open-access electronic publication of journal articles has begun in the biological sciences (<http://www.doaj.org/>), even sharing archived data supplements to papers, which are not printed because of cost and space issues (Vision, 2010). For the most part, however, botany has lagged behind, despite current examples of online publications (*Constancea*, <http://ucjeps.berkeley.edu/constancea/>, The Jepson Manual, <http://ucjeps.berkeley.edu/jepson_flora_project.html>, *Phytotaxa*, <http://www.mapress.com/phytotaxa>, *Phytoneuron*, <http://www.phytoneuron.net/>, and *Vulpia*, <http://www.cals.ncsu.edu/plantbiology/ncsc/vulpia>), and even earlier attempts at computerization (Krauss, 1973). Currently, the issue of valid and effective paperless publication of botanical names is under consideration, predicated by an International Association of Plant Taxonomy's (IAPT) special committee report (Chapman et al., 2010).

Even earlier, before pre-print status (or post-print, see Harnad, 2003a) of a manuscript, the internet enabled the shift from the trade model (i.e., traditional, restricted commercial publishing) to an online collaborative model for peer review (Harnad, 1996, 2003b; Wilson, 2001). Editors of botanical literature routinely seek scientific reviews by specialists familiar with the concerned plant family and geographic region. To utilize a worldwide audience of reviewers and to connect authors and readers (Tenopir, 1995), taxonomic treatments should be provided online at all stages of preparation and revision (in certain cases after initial editing, e.g., international floras where the author's native language differs from that of the flora).

Digital libraries provide an answer to overuse of paper and declining funding and bookshelf space. Yet for those who still wish to own a personal, printed copy of a particular book, print on demand (POD) is available (Black, 2011) and is becoming an economical alternative (e.g., <http://www.printondemand.com>); however, these are not always of the same print quality and POD can contractually confound issues of copyright and intellectual property, though these problems are becoming less common. If the copyright issue of providing digital access could be solved for all new publications, it would greatly help botanists.

Electronic paper (Heikenfeld et al., 2011; e.g., <http://en.wikipedia.org/wiki/Amazon_Kindle>) is increasingly popular. Tablet platforms have exploded within the past year, e.g., Motorola's Xoom with Android's 3.0 Honeycomb competitive with Apple's iPad. Botanists have not yet tapped the potential for floristic apps for smart phones and tablets as field tools.

Conventional floras are not designed for use in the field, yet many botanists want to be able to identify plants in the field. Imagine the possibilities of having a flora on a smart phone or tablet and not needing internet access as required by a search engine. Apps extend the taxonomic reach in the field. If the device can be charged, a taxonomist can manage without the internet as long as the flora is loaded. Additionally though, internet access can provide supplemental information (e.g., electronic keys, digitized photos and illustrations, specimen data, etc.).

However, it is noted that some people still prefer carrying around books in which they can occasionally press a specimen within pertinent pages. Other issues include the readability of electronic display screens in bright daylight, the electricity requirements of devices (at least for charging or batteries), cost to produce computers as compared to paper, and long-term archiving (although the Internet Archive is noted here: <http://www.archive.org/>).

Digital Floras

When paper publications are digitized, previously unavailable functions, such as full text searching and hyperlinking, become possible (Rosatti & Duncan, 1995; Heidorn, 2004; Kirkup et al., 2005; Kress & Krupnick, 2006). Online floras are now providing multiple-field searches into the data (see Brach & Song, 2006), which allow searching by taxon name or distributional fields, such as elevation, province, and country, as well as searches through free text (<http://www.efloras.org/search_page.aspx?flora_id=2>) and linking treatments to related information, photos and illustrations, maps, databases, checklists, and other floras (Funk, 2006). In addition to full text or "context searching," digital floras also allow for updating with new revised treatments as they become available instead of having to wait for the next paper flora to be published. Data extractions of florulas for geographical areas of special interest, e.g., at a country, state/

province, or county level, are facilitated by digitization (see Kartesz, 2011).

Botanists are challenged to create interactive identification keys (see Dallwitz et al., 2000 onwards; Brach & Song, 2005, <http://flora.huh.harvard.edu/china/ActKey/>; Kuoh & Song, 2005, http://www.efloras.org/key_page.aspx?set_id=10083&flora_id=1050; also e.g., Neotropikey: <http://www.kew.org/science/tropamerica/neotropikey.htm>). They can provide images to be utilized (e.g., Tropicos image search, <http://www.tropicos.org/ImageSearch.aspx>; Biodiversity of the Hengduan Mountains, <http://hengduan.huh.harvard.edu/fieldnotes>) by an online audience of students, researchers, and the general public worldwide.

AN EXAMPLE: THE FLORA OF CHINA

The Flora of China Project (FOC; <http://www.foc.org>) provides online treatments for vascular plants at all manuscript stages (<http://flora.huh.harvard.edu/china/mss/alphabetical_families.htm>) prior to paper publication of text volumes. Draft manuscripts are noted as such in the header, uploaded to the Web site as HTML files, and replaced with revised versions until considered final for volume publication. Once a particular volume is sent to the printer, the final manuscripts for the volume are then databased (<http://www.eFloras.org>, see Brach & Song, 2006). Because of this dynamic accessibility, we regularly receive e-mail from the general public asking about plant identification and use, as well as from specialists worldwide, suggesting corrections and inquiries for particular taxa. Also, after printed publication, the project's editors and coauthors, and specialists outside of the project have the opportunity to submit corrections, which we have routinely incorporated into both the databased, published treatments accessible via an interface on <http://www.eFloras.org> and into the project's database of corrigenda for published volumes. Newly published names not available in the printed version are added to the eFloras database and to the FOC Checklist (<http://www.tropicos.org/Project/FC>), also see Brach & Song, 2006). The checklist is maintained as a project within the Web-accessible Tropicos (<http://www.tropicos.org/>). Because the database is regularly updated with corrections, flora users access a "dynamic" flora via the eFloras interface (while the family PDFs are currently maintained in "static" form so as to provide the original, published treatment). Questions for the future will include how to manage major revisions of families and genera after "print publication" of volumes, alternative treatments by authors differing in their taxonomic opinions, and authorship of revisions to the database years later.

The FOC Project provides interactive identification keys (Brach & Song, 2005) in DELTA Intkey and NaviKey formats (<http://flora.huh.harvard.edu/china/ActKey/>). Electronic keys are available for large genera (generally 50 or more species, but also for some smaller genera). The DELTA data are archived and accessible (<http://www.species-id.net/wiki/Main_Page>) for updates and improvements. The keys can be modified (characters/states and items/taxa) using the DELTA Editor application, and subsequent revised keys posted online.

DEVELOPMENTS IN DIGITIZING FLORAS

Existing natural language descriptions can be parsed by software such as MARTT (Markuper of Taxonomic Treatments) (Cui, 2008) into XML language (demonstrated at <http://research.sbs.arizona.edu/~hongc/ResearchDemo/MARTTDemo1.html>), thereby providing searchable databases online (<http://research.sbs.arizona.edu/gs/cgi-bin/library>).

For new and revised editions of floras, digital floras should be created starting at the beginning of any new project. Programs such as DEscription Language for TAxonomy (DELTA, Dallwitz, 1980; Dallwitz et al., 1993 onwards; Brach & Song, 2005) provide tools (cf. the DELTA Editor: <http://delta-intkey.com/www/delta-ed.htm>) for inputting characters, character states, measurements, and counts into data matrices to then output as natural language descriptions (in which natural language descriptions read as a natural language and not as machine-generated) and interactive identification keys that can be linked to related images. Open repositories for interactive key datasets (see <http://www.species-id.net/wiki/Main_Page>) may be used as examples in building new character sets and interactive keys and in creating new data conversion (Structure of Descriptive Data, SDD; DELTA, etc.) and input utilities, and also to provide an archive for the data. Also, digital image libraries of taxa can be implemented as part of the identification process (Agarwal et al., 2006; Hearn, 2009; also Wikispecies, <http://species.wikimedia.org/> and Wikimedia Commons, <http://commons.wikimedia.org/>).

With pressing issues of cataloguing biodiversity, conservation, and sustainable use of resources, botanists are now challenged to routinely prepare and revise online treatments, including interactive identification keys and images for a worldwide audience of students and researchers. As botanists,

we should ask ourselves if it is justifiable to continue to produce printed books on paper while at the same time the world is rapidly digitizing older works, and when it appears that soon an increasing number of new works will be available in digital format. Although advances in book scanning, electronic publication, and digital libraries are providing the tools and resources to accomplish this, one has to ask what continuing role the printed flora plays.

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TAXONOMIC STUDY OF *GYMNOPOGON* (POACEAE, CHLORIDOIDEAE, CYNODONTEAE)[1]

Ana María Cialdella[2] *and Fernando Omar Zuloaga*[2]

Abstract

The present paper includes a taxonomic revision of the genus *Gymnopogon* P. Beauv. (Poaceae, Chloridoideae, Cynodonteae), with a total of 14 species treated in this work, including more than 40 synonyms. The genus includes perennial, occasionally annual, species, with erect to decumbent culms, ligules membranous-ciliate, blades conspicuously distichous, inflorescences with spikelets on racemiform branches, spikelets laterally compressed, 1- to 4-flowered, glumes 1-nerved, lemma 3-nerved, awned. Species distributions are mostly American, with one Asian species. A description of morphological characters, key to identify the species, descriptions, synonymy, geographical distribution, and illustrations of characteres of taxonomic value are also included. The name *Chloris delicatula* C. B. Clarke ex Hook. f. (≡ *Gymnopogon delicatulus* (C. B. Clarke ex Hook. f.) Bor) is lectotypified.

Resumen

El presente trabajo consta de una revisión taxonómica de las especies del género *Gymnopogon* P. Beauv. (Poaceae, Chloridoideae, Cynodonteae). En este manuscrito se trata un total de 14 especies, incluyendo más de 40 sinónimos. El género incluye especies perennes, ocasionalmente anuales, con tallos erectos a decumbentes, lígulas membranáceo-ciliadas, láminas conspicuamente dísticas, inflorescencias con espiguillas sobre ramas racemiformes, las espiguillas lateralmente comprimidas, 1- a 4-floras, glumas 1-nervias, lemma 3-nervia, aristada. En lo que se refiere a la distribución geográfica, las especies son mayormente americanas, con una especie asiática. Se incluye la descripción de caracteres morfológicos, una clave para identificar las especies, descripciones, sinonimia, distribución geográfica e ilustraciones de los caracteres de valor taxonómico. Asimismo, se ha designado un lectotipo para *Chloris delicatula* C. B. Clarke ex Hook. f. (≡ *Gymnopogon delicatulus* (C. B. Clarke ex Hook. f.) Bor.

Key words: Chloridoideae, Cynodonteae, *Gymnopogon*, Poaceae.

The genus *Gymnopogon* P. Beauv. (Poaceae) was established by Palisot de Beauvois in 1812, on the basis of *Andropogon ambiguus* Michx. *Gymnopogon* belongs, within subfamily Chloridoideae, to tribe Cynodonteae Dumort., which includes taxa with spiciform geminate racemes; spikelets subsessile or sessile, unilaterally distributed in one or two series along the rachis of the racemes; 1-flowered spikelets, exceptionally with more florets; the rachilla generally disarticulated above the glumes; the glumes, lemmas, and paleae membranous; and the lemmas 3-nerved, awnless, mucronate, or 1- to 3-awned. Within this tribe, *Gymnopogon* is related to *Chloris* Sw., as both genera share a rachilla extension behind the upper developed floret, spikelets usually with one fertile floret, and the lemmas awnless or with a subapical awn. *Chloris* differs by its inflorescences arranged in terminal digitate clusters, rarely with one or more branches below; spikelets densely imbricate along the rachis; and the glumes equal to or shorter than the floret. Moreover, the genus *Chloris* does not present conspicuously distichous leaves along the culms as can be found in *Gymnopogon*.

Gymnopogon has been scarcely scrutinized in regional or partial treatments, with the exception of the revision published by Smith (1971), who recognized 13 species, one subspecies, and one form. *Gymnopogon* has been considered only in regional floras: Hitchcock (1930) cited two species for Central America: *G. aristiglumis* Hitchc. and *G.*

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fastigiatus Nees. Swallen (1955) reported *G. spicatus* (Spreng.) Kuntze for Guatemala, and Bor (1960) mentioned the unique Asian species, *G. delicatulus* (C. B. Clarke ex Hook. f.) Bor, from Myanmar (Burma) and India. Burkart (1969) mentioned two species for Entre Ríos, Argentina: *G. spicatus* and *G. biflorus* Pilg. [= *G. spicatus*]. Rosengurtt et al. (1970), when treating the grasses of Uruguay, included four species for the genus: *G. burchellii* (Munro ex Döll) Ekman, *G. grandiflorus* Roseng., B. R. Arill. & Izag., *G. legrandii* Roseng., B. R. Arill. & Izag., and *G. biflorus*. Caro (1982) described a new species, *G. glaber* Caro. Boechat and Valls (1990b) studied *Gymnopogon* for Brazil and included in their revision seven species, among them *G. doellii* Boechat & Valls, endemic to that country. Davidse et al. (1994) treated three species for Mesoamerica: *G. spicatus*, *G. fastigiatus* subsp. *fastigiatus*, and *G. aristiglumis*. Renvoize (1998), in his account of the grasses of Bolivia, cited three species for the country: *G. burchellii*, *G. fastigiatus*, and *G. spicatus*. Smith (2003) mentioned three species for the *Flora of North America*: *G. brevifolius* Trin., *G. ambiguus* (Michx.) Britton, Sterns & Poggenb., and *G. chapmanianus* Hitchc. Finally, Sulekic and Rúgolo de Agrasar (2006) described a new species of *Gymnopogon* from Argentina and provided a key to distinguish the northwestern species of the genus in that country.

Pilger (1956) considered two sections in the genus: section *Gymnopogon*, which included species with a pilose callus, and section *Monochaete* (Döll) Pilg., which included *G. fastigiatus* and *G. jubiflorus* Hitchc., the latter section characterized by including species with a glabrous callus. Originally, Döll (1878) defined section *Monochaete*, with a single species, *G. fastigiatus*, by not having the rachilla prolonged into an awn, but this character is not useful to delimit infrageneric boundaries in *Gymnopogon*.

Gymnopogon is principally defined by its distichous leaves; the inflorescences with long, spiciform branches; the axis of the branches naked toward the base; and the spikelets laterally compressed, 1- to 4-flowered, with the lemma awned. Within the genus, its species can be distinguished by morphological characters, such as the rhizome shape in perennial species; the length of spiciform racemes; whether floriferous or naked at the base; awned or awnless glumes, lemmas, and rachilla, with the latter with one or more awnlike rudiments at the apex; and the floret size.

Gymnopogon comprises 14 species and two subspecies, all distributed in the Americas, with the exception of *G. delicatulus*, an Asian species. In this paper, we present a taxonomic account of the entire genus, based on exomorphological, vegetative, and reproductive characters; provide a key to identify species and subspecies; include associated synonymies; and consider geographical distributions, descriptions, and illustrations of taxonomically valuable features for all recognized taxa within the genus.

Material and Methods

This study was based on the morphological analysis of almost 300 herbarium specimens, including type material when available or digital images when these specimens could not be loaned for study. Examined specimens were from the following herbaria, cited according to abbreviations from Holmgren et al. (1990): BA, BAA, BAB, BM, CEN, CORD, CTES, G, IBGE, ICN, K, LE-TRIN, LPB, MO, MVFA, NY, SI, and US. The institutions that kindly supplied digital images of the type material were: CEN, G, Board of Trustees of RBG Kew (K), MVFA, P, and US. A list of examined specimens is provided in Appendix 1.

Taxonomic Treatment

Gymnopogon P. Beauv., Ess. Agrostogr. 41, 164. 1812. TYPE: *Andropogon ambiguus* Michx. [≡ *Gymnopogon ambiguus* (Michx.) Britton, Sterns & Poggenb.].

Anthopogon Nutt., Gen. N. Amer. Pl. [Nuttall] 1: 81. 1818, nom. illeg. superfl. TYPE: *Andropogon ambiguus* Michx.

Biatherium Desv., Mém. Soc. Agric. Angers 1: 172, t. 8, f. 2. 1831. *Biatherium foliosum* (Willd.) Desv., Mém. Soc. Agric. Angers 1: 176, t. 8, f. 2. 1831.

Doellochloa Kuntze, Revis. Gen. Pl. 2: 773. 1891, nom. illeg. superfl. TYPE: *Doellochloa fastigiata* (Nees) Kuntze [≡ *Gymnopogon fastigiatus* Nees].

Monochaete Döll, Fl. Bras. (Martius) 2(3): 78. 1878. *Gymnopogon* sect. *Monochaete* (Döll) Pilg., Nat. Pflanzenfam., ed. 2 [Engler & Prantl] 14d: 94. 1956. Based on *Monochaete fastigiata* (Nees) Döll, Fl. Bras. (Martius) 2(3): 79. 1878.

Caespitose or rhizomatous perennials, with short rhizomes, occasionally annuals; culms erect to decumbent, rigid, simple or scarcely branched at the base, internodes terete; nodes slightly thickened or narrowed. Leaf sheaths usually longer than the internodes, striate, strongly overlapping, pilose or glabrous; ligules membranous-ciliate; blades lanceolate to linear-lanceolate, conspicuously distichous, flat, convolute or involute, narrowed or subcordate at the base, the apex apiculate. Inflorescence terminal, open, with several spreading racemes on alternate or opposite branches, axis of the branches naked at the base or floriferous throughout, triquetrous, scabrous,

with appressed, alternate spikelets toward the apex, main axis ending in a raceme. Spikelets shortly pedicellate, laterally compressed, tight against the rachis, 1- to 4-flowered with 1 to 2 lower perfect florets and 1 or 2 neuter or reduced upper florets; rachilla articulated above the glumes. Glumes 2, longer than the florets, 1-nerved, the nerve scabrous, acuminate; lemma 3-nerved, pubescent or glabrous, lateral nerves proximal to the margins, the apex acute or minutely bifid, aristate, the awn straight, usually longer than the bracts of the spikelet, occasionally muticous; palea membranous, 2-nerved; rachilla prolonged beyond the upper floret, ending in an awn; stamens 3, occasionally 2; lodicules 2, cuneate; gynoecium with 2 styles and 2 plumose stigmas. Caryopsis fusiform, hilum punctiform, embryo 1/3 or less the length of the caryopsis.

Distribution. *Gymnopogon* is a genus with 14 species, mostly from the New World, distributed from the United States to Argentina, with one species in the Old World (*G. delicatulus*). Species of *Gymnopogon* are of low forage value and are found in tropical and temperate areas, usually on dry and sandy soils. According to Parodi (1919), these chloridoid grasses contribute to the establishment of natural prairies.

Key to the Species of *Gymnopogon*

1a. Glumes awned or with a short awnlike acumen 0.5 mm or longer in both or one of the glumes 2
1b. Glumes awnless 3
2a. Glumes with an awn 3–7(–15) mm; main axis of the inflorecescence 15–20 cm; lemma of the lower floret sparsely villous toward the margins, otherwise glabrous; collar glabrous ..... 2. *G. aristiglumis*
2b. Glumes acuminate or with an awn 0.5–2.5(–3) mm; main axis of the inflorescence 9–16 cm; lemma of the lower floret usually pilose in the dorsal portion and margins; collar densely villous all over or only at the margins..... 13. *G. spicatus*
3a. Lemma and rachilla awnless ..... 4. *G. burchellii*
3b. Lemma and rachilla awned 4
4a. Branches of the inflorescences with developed or reduced spikelets from the base..... 5
4b. Branches of the inflorescences without spikelets at the base..... 11
5a. Plants perennial with stoloniform rhizomes..... 12. *G. legrandii*
5b. Plants annual or perennial with short and thickened rhizomes..... 6
6a. Lemma awn (1–)1.5(–2) mm, occasionally awnless, but with the rachilla always ending in an awnlike rudiment 0.8–3 mm... 5. *G. chapmanianus*
6b. Lemma awn (3–)4.5–33 mm..... 7
7a. Lower, or unique in single-flowered spikelets, floret 1.4–2.3 mm 8
7b. Lower, or unique, floret 2.4–4(–5.5) mm..... 10
8a. Apex of the rachilla ending in an awnlike rudiment up to 0.5 mm; lemma with hairs 0.3–2 mm at the distal 1/3 of the margins; lemma awn hygroscopic; perennial plants..... 8. *G. fastigiatus*
8b. Apex of the rachilla ending in 2(3) awnlike rudiments 3.8–15 mm; lemma glabrous or with hairs 0.1–0.3 mm; lemma awn not hygroscopic; annual plants 9
9a. Lemma 1.6–2.3 mm, glabrous, with a subapical awn (7–)8.5–23 mm; Caribbean and northern South America ..... 9. *G. foliosus*
9b. Lemma ca. 1.4 mm, with whitish hairs 0.1–0.3 mm at the margins and scattered on the base, mainly on the middle nerve; southern Asia..... 6. *G. delicatulus*
10a. Lemma awn 7–12 mm; callus subglabrous; floret 2.4–3.1 mm; Brazil..... 7. *G. doellii*
10b. Lemma awn 5–6 mm; callus villous; floret 3–4 mm; central and southeastern United States and Caribbean..... 1. *G. ambiguus*
11a. Lemma awn (18–)24–25(–33) mm; ligules 0.5–0.8 mm..... 14. *G. toldensis*
11b. Lemma awn 1–9(–12) mm; ligules 0.1–0.5 mm 12
12a. Lemma awn 1–2 mm; surface of the lemma with short hairs on the middle nerve and toward the margins, sometimes scattered on the whole surface..... 3. *G. brevifolius*
12b. Lemma awn 5–9(–12) mm; surface of the lemma glabrous or with scarce short hairs scattered on the basal portion 13
13a. Lemma of the lower floret 3.5–4(–5.5) mm, generally with short hairs; lower glume 3.5–5 mm, upper glume 4.5–5.5 mm ... 11. *G. grandiflorus*
13b. Lemma 2–3 mm, glabrous; lower glume 3–3.5 mm, upper glume 4–4.5 mm ..... 10. *G. glaber*

Species Treatment

1. Gymnopogon ambiguus (Michx.) Britton, Sterns & Poggenb., Prelim. Cat. 69. 1888. Basionym: *Andropogon ambiguus* Michx., Fl. Bor.-Amer. (Michaux) 1: 58. 1803. *Gymnopogon racemosus* P. Beauv., Ess. Agrostogr. 41, 164, t. 9, fig. 3. 1812, nom illeg. superfl. TYPE: [United States]. "In sabulosis Carolinae," s.d., *A. Michaux s.n.* (holotype, P not seen, P photo at SI!; isotype, P not seen, P photo at SI!). Fig Gen. N. Amer. Pl. [Nuttall] 1: 82. 1818, nom. inval., pro syn. *Gymnopogon racemosus* P. Beauv.

Gymnopogon scoparius Trin., Gram. Unifl. Sesquifl. 237. 1824. TYPE: United States. "V. Sp. e New Jersey, Nov. Coesar," 1835, *A. Gray s.n.* (holotype, LE-TRIN-2123.01!).

Alloiatheros ambiguus (Michx.) Elliott ex Kunth, Enum. Pl. [Kunth] 1: 284. 1833. *Alloiatheros ambiguus* Elliott ex B. D. Jacks., Index Kew. 1: 83. 1893, nom. inval., pro syn. *Gymnopogon racemosus* P. Beauv.

Alloiatheros lepturoides (Nutt.) Steud., Nomencl. Bot. [Steudel] ed. 2: 55. 1840, nom. inval., pro syn. *Gymnopogon racemosus* P. Beauv.

Stipa expansa Willd. ex Steud., Nomencl. Bot. [Steudel] (ed. 2) 2: 643. 1841, nom. inval., pro syn. *Gymnopogon racemosus* P. Beauv.

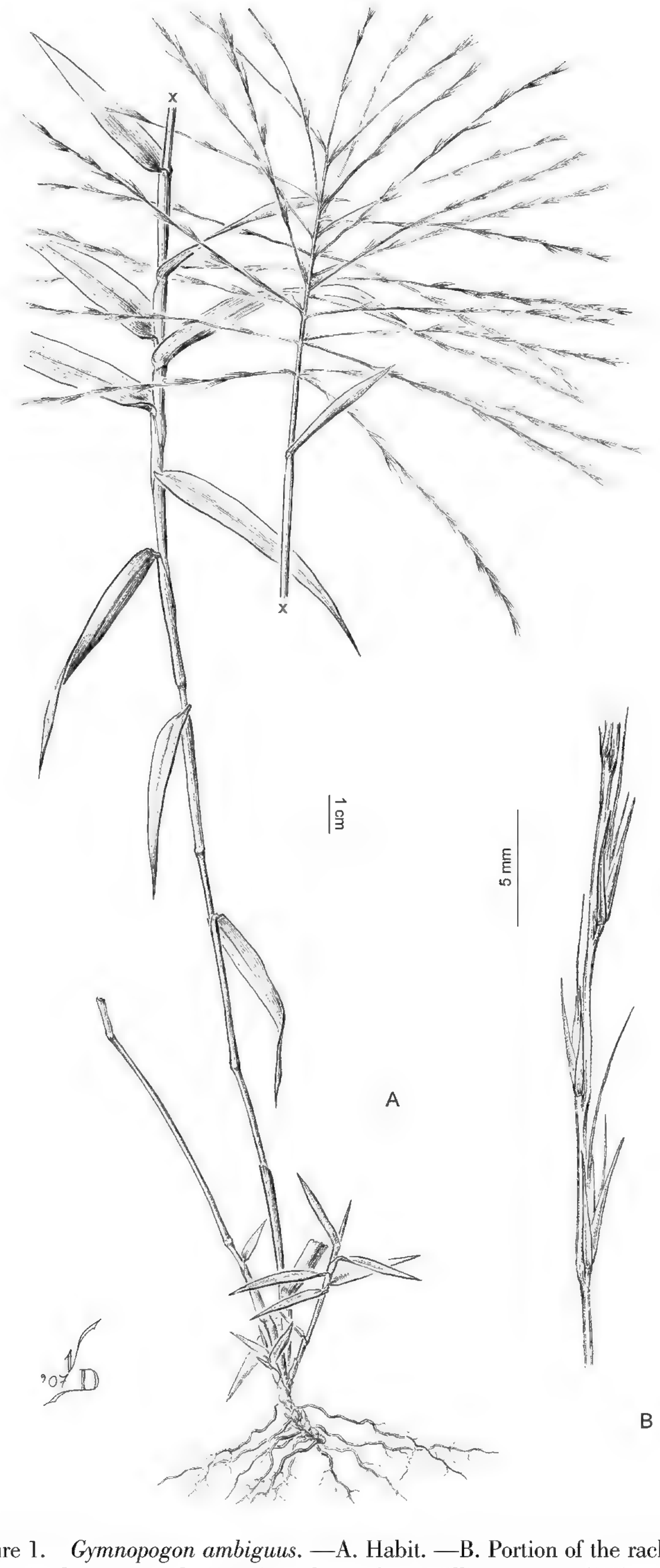

Figure 1. *Gymnopogon ambiguus*. —A. Habit. —B. Portion of the rachis with spikelets. —C. Spikelet. —D. Floret, dorsal view. —E. Floret, ventral view. A–E drawn from *Williamson s.n.* (NY).

Plants perennial, shortly rhizomatous, rhizomes 1.5–2 cm, from which several aerial culms develop; culms 20–100 cm, 1–1.2 mm diam., terete, robust, tufted, simple, erect or decumbent and geniculate; internodes yellowish to brownish, somewhat thickened toward the nodes, longitudinally striate, glabrous; nodes brownish, glabrous; floriferous culms terete, glabrous, striate and hispid toward the apex. Basal sheaths longer than the internodes, the upper ones shorter, striate, yellowish to brownish, glabrous, with smooth and glabrous margins; ligules 0.1–0.2 mm, membranous-ciliate; pseudoligule, a few macrohairs ca. 1 mm; collar conspicuous, yellowish or brownish, strongly narrowed and with long hairs toward the margins; blades lanceolate, rarely oblong, 4–5.5(–9) × 0.3–0.7(–1.5) cm, distichous, ascendent or divergent, convolute or flat, broadly

Figure 2. *Gymnopogon aristiglumis*. —A. Habit. —B. Spikelet. —C. Glumes. —D. Spikelet detached from glumes. A–D drawn from *Calderón 2072* (NY).

subcordate, acute, longitudinally striate and glabrous on both surfaces, the margins scabrous. Inflorescence of (8 to)15 to 25(to 36) spiciform racemes, 10–20(–29) cm, ascending or divergent, alternate; main axis triquetrous, (6–)10–15(–25) cm, glabrous, the angles scabrous; rachis of the racemes triquetrous, ca. 0.2 mm wide, straight, yellowish to brownish, glabrous, with scabrous angles, floriferous from the base, with basal spikelets developed or reduced. Spikelets fusiform, laterally compressed, 4.5–5.5 mm, 1-flowered, rarely 2-flowered, tight against the rachis, subsessile, alternate and distant in 2 series along the rachis; pedicels 0.4–0.5 mm, scabrous. Glumes subequal, 4–5.5 mm, longer than the floret, membranous, yellowish to brownish, 1-nerved, slightly indurated, awnless, glabrous, scabrous along the nerve; floret shortly stipitate, callus near 0.2 mm, villous; lemma membranous 3–4 mm, 3-nerved, the lateral nerves inconspicuous near the margins, minutely bifid at the apex, yellowish, pilose toward the margins, otherwise glabrous, with a subapical, straight awn 5–6

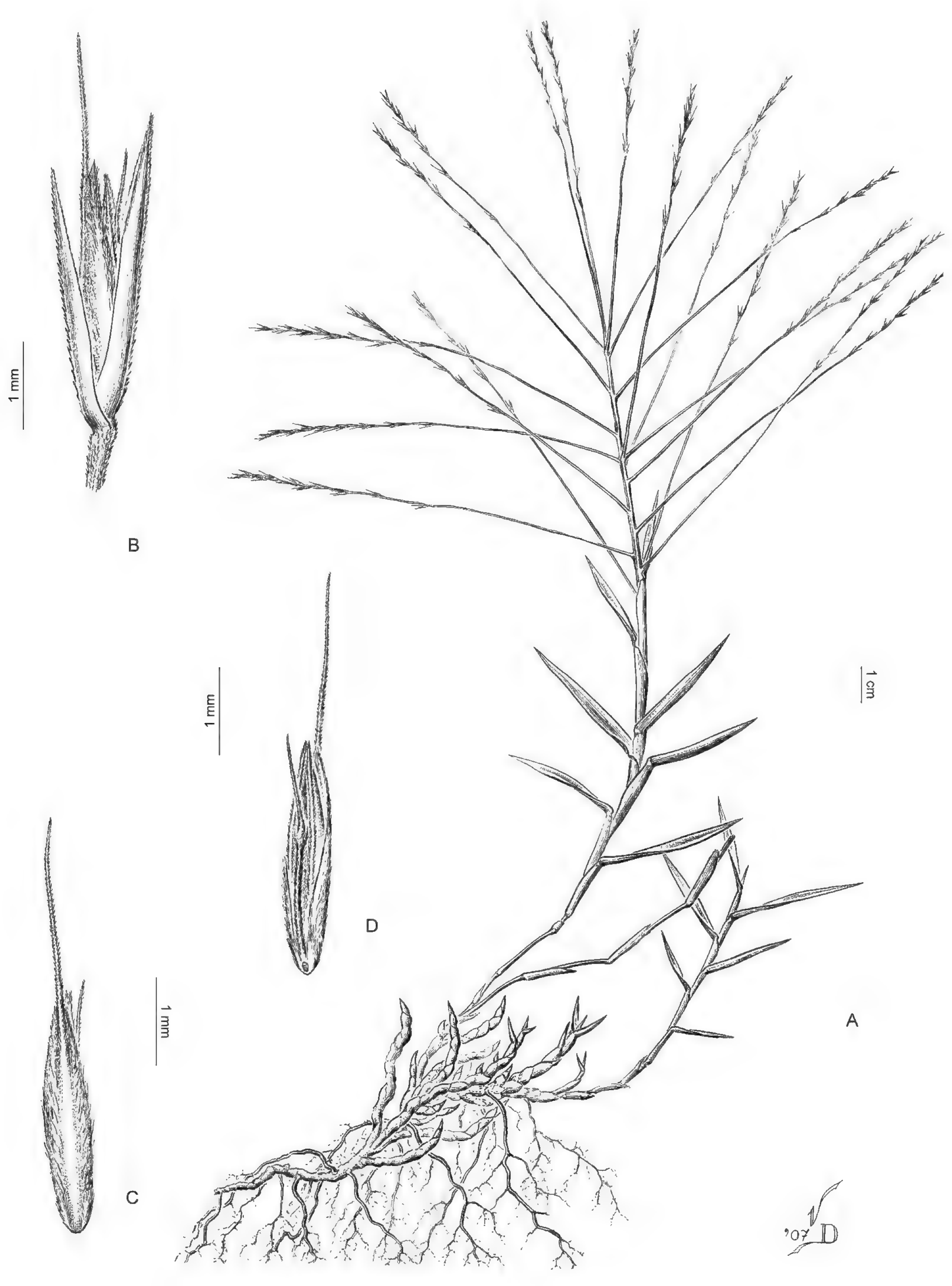

Figure 3. *Gymnopogon brevifolius*. —A. Habit. —B. Spikelet. —C. Floret, dorsal view. —D. Floret, ventral view. A–D drawn from *Thomas 103070* (NY).

mm, scabrous; palea membranous, pale, 2-nerved, ca. 1.8 mm, sparsely pilose at the apex, otherwise glabrous; rachilla extended behind the floret, terete, ca. 1.5 mm, glabrous, its apex bearing an awnlike rudiment ca. 4.5 mm, geniculate near its base, scabrous. Caryopsis fusiform, 2.2–2.3 × 0.3–0.4 mm; embryo less than 1/3 the length of the caryopsis, hilum basal, punctiform.

Distribution and habitat. *Gymnopogon ambiguus* is found in the central and southeastern United States to the Caribbean, in Haiti and the Dominican Republic. It is frequent in dry, sandy soils in pine woods, from sea level to 1600 m. The taxon has been observed to flower between August and November.

Observations. *Gymnopogon ambiguus* is similar to *G. doellii*, as they share inflorescence branches floriferous from the base, with spikelets 2.4–5.5 mm. *Gymnopogon doellii* can be distinguished by its smaller florets (2.4–3.1 mm vs. 4.5–5.5 mm in *G. ambiguus*), with a subglabrous callus (vs. villous), glumes 5.1–9.6 mm (vs. 4–5.5 mm) and lemma awns 7–12 mm (vs. shorter ones, 5–6 mm in *G. ambiguus*). The distribution range of both species also differs: *G. ambiguus* is the most frequent species collected in the United States, while *G. doellii* is restricted to southeastern Brazil.

Some specimens of *Gymnopogon ambiguus* have been confused with *G. chapmanianus*; both species have large spikelets, but in *G. chapmanianus* they are 2(to 3)-flowered, making the spikelets appear wider and the glumes open. *Gymnopogon chapmanianus* is found in the southern United States.

Representative specimens examined. DOMINICAN REPUBLIC. **Barahona:** Trail betw. Pedernales & Aceitial, *Howard 8138* (BM). HAITI. Mornes des Commissaires, *Holdridge 1215* (NY), *1715* (BM). U.S.A. **Alabama:** Sandy rise in Choctawhatchee bottoms by Ala. 85, S of Daleville, *Kral 69705* (BM). **Arkansas:** Miller Co., along Ark. 237 & in cemetery of Macedonia Baptist Church, 0.7 mi. N of Ark. 160 NW of Doddridge, *Thomas et al. 151215* (NY). **Florida:** Braidentown, *Tracy 7766* (BM); Dunedin, *Tracy 7764* (BM, NY). **Georgia:** Elbert Co., Stinchcomb Church rd., *Coile 1582* (BM). **Indiana:** Daviess Co., 5 mi. S of Plainville, *Potzger 10649* (NY). **Kansas:** Sandy woods, Chautauqua Co., *Hitchcock 906* (NY). **Kentucky:** Dry fields in Croppie Hollow Development, on Ky. 614, *Athey 2186* (NY). **Louisiana:** Kisatchie Natl. Forest, compart. 48, stand 7, *Thomas 147645* (NY); at Sizemore pond area, Jackson-Bienville Refuge, *McArdle 424* (BAA). **Maryland:** Salisbury, *Canby 14981* (BM); Great Falls, *Ball 80* (NY). **Mississippi:** Holmes Co., *McGee 1384* (NY). **Missouri:** Monten Mo., *Bush 7883* (NY). **New Jersey:** Burlington Co., 1.5 mi. NW of Green Bank, *Koster C5206-1* (BM). **North Carolina:** Madison Co., sandy soil near Paint Rock, *Biltmore 475c* (NY). **Ohio:** Jackson Co., *Pontious & Bartley 34* (NY). **Oklahoma:** Sapulpa, *Bush 1340* (NY). **Philadelphia:** s. loc., s.d., *Nuttall s.n.* (BM). **South Carolina:** Berkeley Co., Santee Canal, 5 mi. W of Pineville, *Godfrey & Tryon 1597* (NY). **Tennessee:** Barrens at Tullahoma, Aug. 1886, *Gatingen s.n.* (NY). **Texas:** Beckville, 1902, *Reverchon s.n.* (BM); Jasper Co., U.S. 96, 4.5 mi. S of jct. Texas 146 at Brookeland, *Smith 2474* (BM). **Virginia:** Caroline Co., Royal Fort Fost, *Walker 3222* (BM). **Washington D.C.:** Deanwood, *Hitchcock 660* (NY); in woods on Bunker Hill, Brookland, *Holm s.n.* (NY).

2. Gymnopogon aristiglumis Hitchc., Proc. Biol. Soc. Washington 40: 82. 1927. TYPE: El Salvador. Rosario, Jan. 1924, *S. Calderón 1924* (holotype, US 1169956, US photo at SI!; isotype, BAA 1376!). Figure 2.

Caespitose perennials, rhizomatous, rhizomes 1–1.5 cm, from which several culms develop; culms 70–100 cm, 1 mm diam., terete, slender, simple and decumbent, slightly geniculate at the basal nodes; internodes yellowish to brownish, smooth, glabrous; nodes brownish, slightly thickened, glabrous; floriferous culms terete, longitudinally striate at the apex, glabrous. Sheaths shorter than the internodes, longitudinally striate, yellowish, the margins hyaline and villous toward the apex; ligule membranous-ciliate, 0.1–0.3 mm; pseudoligule, when present, a group of hairs up to 1.5 mm; collar conspicuous, yellowish to brownish, strongly narrowed, glabrous; blades narrowly lanceolate, 4–8(–9) × 0.3–0.5(–1.1) cm, ascendent or divergent, subcordate at the base, acuminate, flat, the margins involute toward the apex, longitudinally striate, glabrous on both surfaces, occasionally the adaxial surface villous at the base and toward the margins, the margins scabrous. Inflorescences partially included in the apical sheath, with 14 to 20 spiciform racemes, (13–)15–20(–40) cm, ascending or divergent, alternate or opposite; main axis 15–20 cm, longitudinally striate, glabrous, the angles scabrous; rachis of the racemes triquetrous, 0.2–0.3 mm, straight, yellowish, the angles scabrous, floriferous from the base, with basal spikelets often reduced to the awned glumes and 1 or 2 awned lemmas. Spikelets fusiform, laterally compressed, 2.3–3 mm, 1- or 2-flowered, tight against the rachis, subsessile, loosely disposed in 2 series along the rachis; pedicels 0.7–0.9 mm, slightly flattened, scabrous. Glumes subequal, 2.3–3 mm, longer than the florets, membranous, violaceous, 1-nerved, glabrous, scabrous along the nerve, with a subapical straight awn 3–7(–15) mm; lower floret shortly stipitate, callus terete, ca. 0.5 mm, glabrous; lemma membranous 2–2.5 mm, 3-nerved, sparsely villous toward the margins, otherwise glabrous, shortly bipartite and laciniate at the apex, with a subapical awn 8–20 mm, straight or slightly geniculate, yellowish to violaceous, hispidulous; palea membranous, equal to the lemma, 2-nerved, shortly laciniate at the apex, glabrous or sparsely pilose; upper floret, when present, similar to the lower one but smaller; rachilla prolonged behind the floret, terete, 1–1.5 mm, scaberulose, the apex ending in an awnlike scabrous rudiment ca. 9 mm. Caryopsis fusiform, 1.7–2.5 mm.

Distribution. *Gymnopogon aristiglumis* has been collected in El Salvador (Cerro San Jacinto, Rosario) between the months of July and November. Smith (1971) cited this species for the department of Santa Cruz in Bolivia, without mentioning any specimens from this country. However, Renvoize (1998) did not include *G. aristiglumis* among the species present in Bolivia.

Observations. *Gymnopogon aristiglumis* and *G. spicatus* share the presence of awned glumes. They differ by the different lengths of the awns, 0.5–2.5(–3) mm in *G. spicatus*, but longer in *G. aristiglumis*, ranging from 3–7(–15) mm.

Representative specimens examined. EL SALVADOR. Cerro de San Jacinto, Nov. 1923, *Calderón 2072* (NY); San Salvador, July 1922, *Calderón 949* (NY).

3. Gymnopogon brevifolius Trin., Gram. Unifl. Sesquifl. 238. 1824. *Anthopogon brevifolius* Nutt. ex Trin., Gram. Unifl. Sesquifl. 238. 1824, nom. inval. pro syn., *Gymnopogon brevifolius* Trin. TYPE: United States. Delaware: s. loc., *Digyn s.n. ex Bernhardi herb.* (holotype, LE-TRIN 2118.01 not seen, LE-TRIN photo at SI!; isotype, MO [2]!). Figure 3.

Anthopogon filiformis Nutt., Trans. Amer. Philos. Soc., n.s., 5: 152. 1837 [1835], as "*filiforme*." TYPE: United States. Arkansas: "in shrubby prairies near the banks of the Arkansas," Apr. 1818, *T. Nuttall s.n.* (holotype, BM not seen; isotype, PH not seen).

Gymnopogon racemosus P. Beauv., Ess. Agrostogr. 41, 164, t. 9, f. 3. 1812, nom. illeg.

Gymnopogon racemosus P. Beauv. var. *filiformis* Chapm., Fl. South. U.S. 556. 1860, nom. inval.

Plants perennial, rhizomatous, rhizomes thin and extended, up to 9 cm, branched, yellowish; culms 1–1.5 mm diam., terete, slender, simple, usually decumbent, erect; internodes yellowish to brownish, inconspicuously striate, glabrous; nodes slightly enlarged, yellowish to brownish, glabrous; floriferous culms terete, brownish, inconspicuously striate, glabrous. Sheaths shorter than the internodes, longitudinally striate, brownish, glabrous, the margins smooth and glabrous, scabrous to villous toward the collar; ligules membranous, 0.1–0.3 mm, the margins densely ciliate; pseudoligule a ring of long hairs, or absent; collar yellowish, conspicuously narrowed, villous at the margins, otherwise glabrous; blades linear-lanceolate, 2–6 × 0.25–0.5(–0.8) cm, distichous and rigid, ascendent or divergent, convolute, involute or flat, conspicuously cordate or truncate at the base, acute, longitudinally striate and glabrous on both surfaces, the margins hispidulous. Inflorescence of (7 to)11 to 12(to 30) divergent spiciform racemes, 9–18 cm, alternate or opposite; main axis triquetrous, 8–10 cm, longitudinally sulcate, brownish, glabrous, the angles hispidulous; rachis of the racemes triquetrous, ca. 0.3 mm wide, brownish, glabrous, hispidulous at the angles, with spikelets on the distal 1/4–1/2 of its length. Spikelets fusiform, 3–3.5 mm, 1-flowered, laterally compressed, tight against the rachis, subsessile, alternate and distant in 2 series along the rachis; pedicels ca. 0.5 mm, slightly flattened, with hispidulous angles. Glumes subequal, 3–3.5 mm, longer than the floret, membranous or slightly indurated, brownish, 1-nerved, the nerve greenish, scabrous along the nerve, awnless, glabrous; floret shortly stipitate, with a blunt callus nearly 0.1 mm, densely villous; lemma membranous 2.4–2.8 mm, 3-nerved, the nerves inconspicuous, pubescent over the middle nerve and the margins, occasionally pubescent on the whole surface, shortly bifid and laciniate at the apex, yellowish, with a subapical awn 1–2 mm, rarely longer, straight, hispidulous; palea membranous, pale, 2-nerved, equal to the lemma, shortly laciniate at the apex, glabrous, the apex hispidulous; rachilla prolonged behind the floret, terete, ca. 1 mm, hispidulous, its apex ending in a short, scabrous, awnlike rudiment. Caryopsis fusiform, 1.8–2 mm, brownish red; embryo less than 1/3 the length of the caryopsis, hilum basal, punctiform.

Distribution and habitat. *Gymnopogon brevifolius* is restricted to the southeastern United States, where it is found in sandy pine woodlands, between sea level and 250 m. It has been noted to flower between August and December.

Observations. *Gymnopogon brevifolius*, *G. legrandii*, and *G. glaber* share the presence of extensive stoloniform rhizomes. *Gymnopogon legrandii* differs from *G. brevifolius* and *G. glaber* by its inflorescences with developed or reduced spikelets from the base of the spiciform racemes. *Gymnopogon glaber* can be distinguished by its lemmas bearing subapical awns 5–7 mm; in *G. brevifolius* awns are shorter, only 1–2 mm, and usually so in *G. legrandii*, 3–3.5(–7) mm. Smith (1971) related *G. brevifolius* with *G. ambiguus*, the latter species being the most frequent one in the United States, but both species grow in sandy woodlands, sharing ecologically similar sites. *Gymnopogon ambiguus* has short, robust rhizomes, from which several vigorous ascendent culms develop, and inflorescences with spiciform racemes that are floriferous from the base, in contrast to the racemes of *G. brevifolius*, which have spikelets restricted to the upper half of the inflorescence axis. Intermediate forms between both species were observed by Blomquist (1948), who suggested possible hybridization between them. Nevertheless, distinguishing characters between these species are: *G. ambiguus*, with basal sheaths longer than the internodes, spikelets 4.5–5 mm long, and lemma awn 5–6 mm long, versus *G. brevifolius*, with basal sheaths shorter than the internodes, spikelets 3–3.5 mm long, and lemma awn 1–2 mm long.

Representative specimens examined. U.S.A. **Alabama:** Cleburne Co., *Kral 44183* (NY). **Arkansas:** Union Co., ca. 3.5 mi. E of New London & 6.5 mi. NW of U.S. 82 E of Strong, Sec 31, T17S, R11W, *Thomas 103070* (NY). **Delaware:** Sussex Co., Sep. 1845, *Ellendale s.n.* (NY). **Florida:** Dade Co., Pineland Prairie, Tamiami Trail, W of Miami, *Small et al. 9388* (NY); dry pine barrens, near Jacksonville, *Curtiss 3442* (BM). **Georgia:** Murray Co., ca. 0.7 mi. W of Chatsworth, S of Market Street, E of jct. Charles Rd., ca. 0.85 rd. mi. W of jct. U.S. Hwy. 411/76, 770 ft., *Allison & Ware 9547* (BM). **Louisiana:** Natchitoches, *Palmer 8876* (NY). **Maryland:** Assateague Island, 1.3 mi. S of bridge cause-way, Rte. 611, State Park, *Hill 15844* (NY). **Mississippi:** Biloxi, *Tracy 4538* (BM). **New Jersey:** Cape May, *Mackenzie 6700* (NY). **North Carolina:** Cumberland Co., 2.5 mi. WNW of Roslin, *Ahles 36570* (NY); Durham Co., Durham, 26 Oct. 1931, *Blomquist s.n.* (NY). **South Carolina:** Charleston Co., Santee Coastal Reserve, Washo Res., S side Santee Gun Club rd., 2.1 mi. E of S Santee rd., *Hill 24537* (NY). **Texas:** Sabine Co., Sabine Natl. Forest, U.S. 96, 13.2 mi. S of Bronson grain elevator, *Smith 2475* (BM). **Virginia:** Nansemond Co., W Railway 1–1.5 mi. W of Kilby, *Fernald 15175* (NY).

4. Gymnopogon burchellii (Munro ex Döll) Ekman, Ark. Bot. 11(4): 35. 1912. Basionym: *Leptochloa burchellii* Munro ex Döll, Fl. Bras. (Martius) 2(3): 93. 1878. *Rhabdochloa burchellii* (Munro ex Döll) Kuntze, Revis. Gen. Pl. 2: 788. 1891. TYPE: Brazil. "In prov. S. Paulo," s.d., *W. J. Burchell 4462* (holotype, K, K photo at SI!; isotypes, BAA-1379!, BR not seen, BR fragm. at US not seen, K fragm. at US not seen). Figure 4.

Gymnopogon muticus Hack., Anales Mus. Nac. Buenos Aires 21 (ser. 3, 14): 117. 1911, nom. nud.

Plants perennial, shortly rhizomatous, rhizomes generally thick, knotty and short, yellowish and glabrous; culms 20–80 cm, 1–1.5 mm diam., terete, slender, erect to decumbent, simple or branched, erect or geniculate at the basal nodes; internodes slightly glaucous, glabrous; floriferous culms terete, hispidulous toward the apex. Sheaths shorter than the internodes, longitudinally striate, yellowish, glabrous or slightly pilose at the margins; collar inconspicuous; ligules 0.1–0.5 mm, membranous, the margin shortly ciliate; pseudoligule occasionally present, with macrohairs up to 2 mm; blades linear, 16–80 × 0.2–0.8 cm, distichous, divergent, flat, conspicuously acuminate, cordate at the base, glabrous on both surfaces, adaxial surface rarely scabrous, the margins scabrous. Inflorescence of 8 to 17 ascendent spiciform racemes, partially included in the upper sheath, 8–21 cm, alternate or grouped; main axis triquetrous, 8–30 cm, glabrous, with scabrous angles; rachis or the racemes triquetrous, 0.2–0.3 mm wide, greenish, glabrous, with scabrous angles. Spikelets fusiform, 1.9–5 mm, laterally compressed, tight against the rachis, subsessile, alternate and distant in 2 series along the rachis, (1 to)2(to 3)-flowered, occasionally with a rudiment of 1 or 2 apical florets with lemmas minutely awned; pedicels 0.3–0.8 mm, flattened, hispidulous. Glumes subequal, longer than the floret, lower glume 1.9–5 mm, upper glume 2.3–5 mm, membranous, yellowish, 1-nerved, slightly indurated and scabrous at the nerve, awnless, glabrous; lower floret shortly stipitate, callus nearly 0.1 mm, glabrous, rarely minutely pubescent; lemma membranous 1.6–2.6 mm, 3-nerved, the lateral nerves inconspicuous and near the margins, shortly bifid at the apex, awnless, violaceous, glabrous or pubescent at the apex; palea membranous, pale, 2-nerved, 1.5–2.1 mm, shortly ciliolate at the margins; upper florets similar to the lower one but smaller; rachilla prolonged behind the upper floret, terete, 0.9–1.5 mm, ending in a minute awnless rudiment. Caryopsis fusiform 1–1.8 × 0.2–0.3 mm; embryo less than 1/3 the length of the caryopsis, hilum basal, punctiform.

Distribution and habitat. *Gymnopogon burchellii* has been collected in natural grasslands of southern Brazil, Paraguay, Uruguay, and Argentina, between sea level and 1300 m. The taxon has been collected in flower between January and May.

Observations. *Gymnopogon burchellii* is easily recognized within *Gymnopogon* by its florets with lemmas and rachilla awnless and the callus generally glabrous. According to collection labels (*Meyer 2294*, *Schulz 1055*, *Schulz 11516*), this species has rhizomes with medicinal properties.

Caro (1982) mentioned the presence of a minute awn, to 0.5 mm, on the lemma of the upper reduced floret, and Boechat and Valls (1990b) cited specimens from Brazil with spikelets bearing up to four fertile florets and a reduced upper floret. However, these characters were not observed in the examined specimens.

Representative specimens examined. ARGENTINA. **Chaco:** Mayor Luis J. Fontana, Ea. Urien, *Schulz 3237* (CTES). **Corrientes:** Capital, "El Piso," *Carnevali 475* (CTES). **Misiones:** Candelaria, Loreto, *Ekman 701* (CORD). BRAZIL. **Distrito Federal:** Gallery forest ca. 25 km SW of Brasília, *Irwin et al. 13073a* (NY). **Mato Grosso:** Vic. of Dourados, *Chase 10962* (BAA). **Minas Gerais:** Lavras, *Chase 8762* (NY). **Paraná:** S. José dos Pinhaes, Rincão, *Hatschbach 3010* (BAA). **Santa Catarina:** Campo Alegre, Bog, lower fazenda of Ernesto Scheide, *Smith & Klein 10530* (NY). PARAGUAY. **Itapúa:** Isla Yacyretá, *Jiménez 14641* (BAA). **Paraguarí:** Caapucú, Est. Barrerito, *Rojas 13174* (BAA). URUGUAY. **Tacuarembó:** Camino a Ribera, a 32 km de Tacuarembó, *Cabrera & Zuloaga 32419* (SI).

5. Gymnopogon chapmanianus Hitchc., Amer. J. Bot. 2: 306. 1915. TYPE: United States. Florida: Seminole Co., Sandford, sandy meadow, 25 Sep.

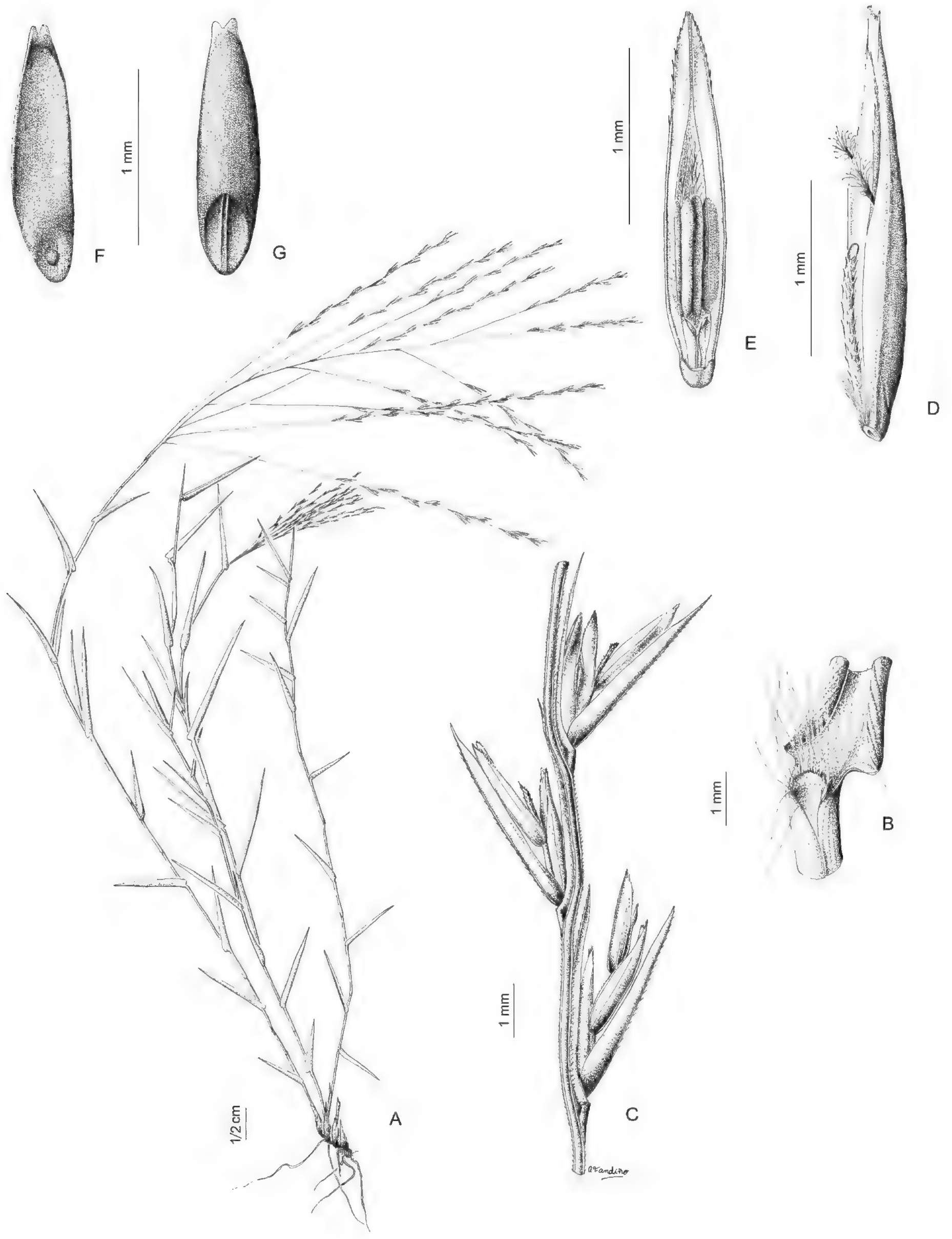

Figure 4. *Gymnopogon burchellii.* —A. Habit. —B. Ligule. —C. Portion of the rachis with spikelets. —D. Floret, lateral view. —E. Floret, ventral view. —F. Caryopsis, hilum view. —G. Caryopsis, scutellar view. A–G drawn from *A. Ragonese 6747* (BAB).

1907, *A. Chase 4135* (holotype, US-733684!, US photo at SI!). Figure 5.

Gymnopogon floridanus Swallen, N. Amer. Fl. 17(8): 607. 1939. TYPE: United States. Florida: Clay Co., collected on open, sandy prairie, Penny Farms, 15 Nov. 1938, *J. R. Swallen 5596* (holotype, US-1723536 not seen, US photo at SI!; isotype, L not seen).

Plants perennial, shortly rhizomatous, rhizomes ca. 1 cm, from which several shoots develop; culms (15–)45–70 cm, 1.4–1.5 mm diam., robust, simple, sometimes loosely branched, ascendent or decumbent, erect; internodes yellowish, finely striate, glabrous; nodes inconspicuous, slightly thickened or narrowed, glabrous; floriferous culms terete, yellowish, inconspicuously striate, glabrous. Sheaths shorter than the internodes, striate, yellowish, the margins pale, smooth and glabrous; ligules ca. 0.5 mm, membranous-ciliate; pseudoligule absent; collar con-

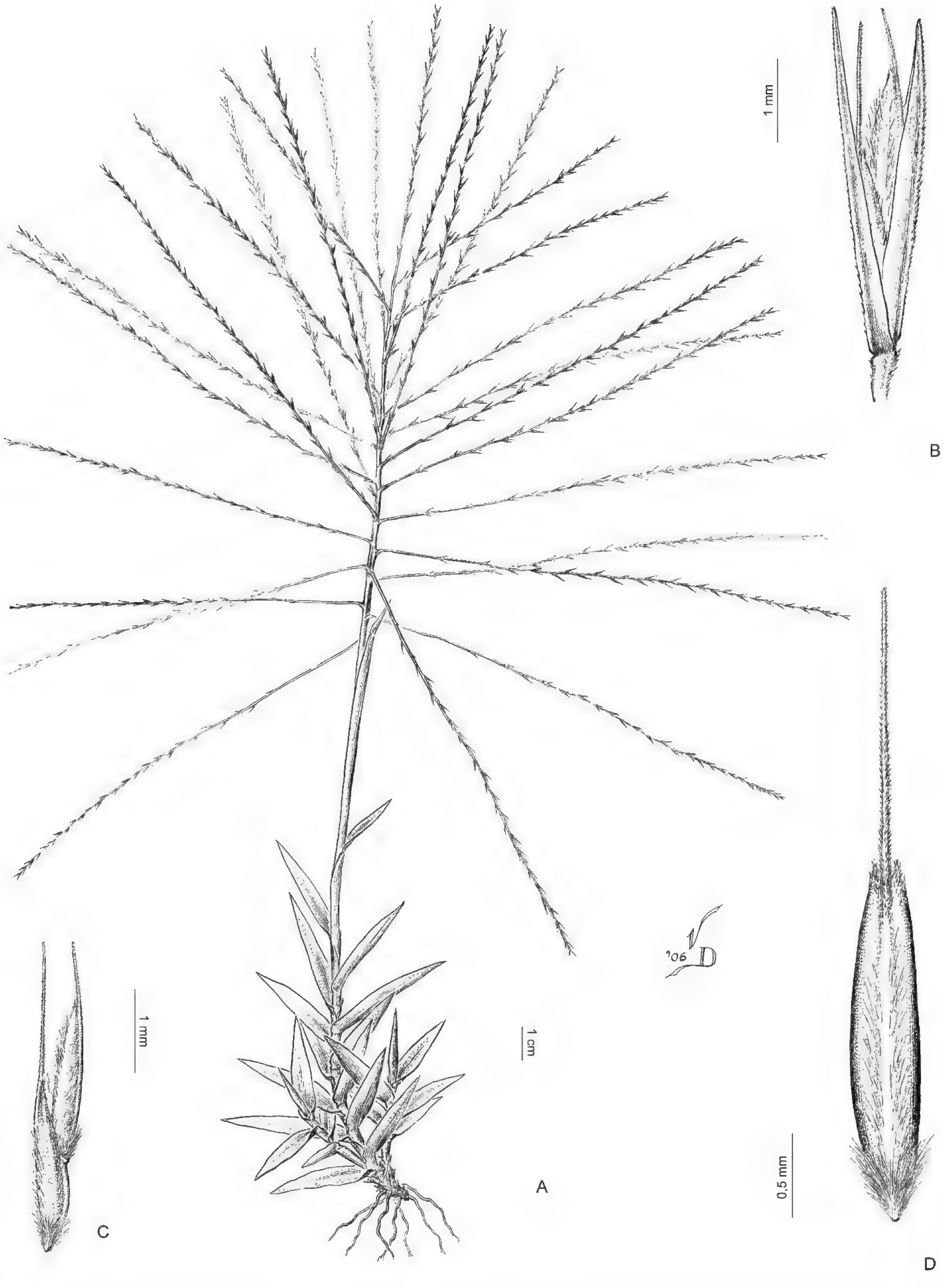

Figure 5. *Gymnopogon chapmanianus*. —A. Habit. —B. Spikelet. —C. Spikelet detached from glumes. —D. Floret. A drawn from *Small & Carter 1030* (NY); B–D drawn from *Curtiss 3441 p.p.* (NY).

spicuous, whitish to reddish, strongly narrowed, glabrous; blades linear-lanceolate, (2.5–)7–8.5 × 0.2–0.5(–0.6) cm, conspicuously cordate, acute or shortly acuminate, distichous on the basal 2/3 of the culms, ascendent, flat, longitudinally striate and glabrous on both surfaces, occasionally scabrous on the abaxial surface, the margins shortly scabrous. Inflorescence of (5 to)15 to 25(to 40) spiciform racemes, (5–)11–20 cm, ascendent or divergent, densely alternate, rarely in pairs; main axis triquetrous, 9–13 cm, brownish, glabrous, the angles scabrous; rachis of the racemes triquetrous, 0.2–0.3 mm wide, brownish, villous at the base, otherwise glabrous, the angles scabrous, floriferous from the base, with reduced basal spikelets. Spikelets fusiform, laterally compressed, (2.5–)4.5–5(–6) mm, 2(to 3)-flowered, subsessile, alternate and distant in 2 series along the rachis; pedicels ca. 0.5 mm, slightly

flattened, scabrous. Glumes subequal, slightly open, lower glume (2.5–)4.5–5(–6) mm, upper glume 3–4(–5) mm, longer than the florets, membranous, violaceous, acuminate, glabrous, with scabrous margins 1-nerved, the nerve yellow greenish and scabrous, slightly indurated, awnless; lower floret shortly stipitate, callus blunt, ca. 0.1 mm, densely villous; lemma membranous, ca. 2 mm, 3-nerved, the nerves inconspicuous, shortly bifid at the apex, violaceous, loosely villous all over the surface, mainly on the middle nerve, with a straight subapical awn, (1–)1.5(–2) mm, scabrous, occasionally awnless; palea membranous, subequal to the lemma, pale, 2-nerved, shortly laciniate at the apex, glabrous; upper florets similar to the lower one, but smaller; rachilla prolonged behind the floret, terete, ca. 1.5 mm, scabrous, its apex bearing an awnlike rudiment 0.8–3 mm, scabrous. Caryopsis not seen.

Distribution and habitat. *Gymnopogon chapmanianus* is restricted to the state of Florida in the southeastern United States. It has been rarely collected and occurs in arid zones. Flowering was recorded between October and November.

Observations. Hitchcock (1915: 307) mentioned that spikelets of *Gymnopogon chapmanianus* can have up to four flowers; however, in the examined specimens, spikelets had up to only three flowers. Hitchcock also mentioned that the dense distribution of the spiciform racemes gives the inflorescence a fanlike aspect. Hitchcock (1951) recognized both *G. chapmanianus* and *G. floridanus* as separate species, and mentioned characters to identify them, such as the position and number of spiciform racemes, and spikelet features, e.g., the glumes wide open in *G. chapmanianus*, leaving the florets visible. Smith (1971), after an exhaustive analysis of herbarium material and field observations, also accepted both species, but suggested a possible hybridization between them due to the presence of intermediate specimens with different combinations of characters cited before, making it difficult to classify them. The variation of reproductive characters between both species makes it reasonable to continue to consider them as one unique entity, and therefore *G. floridanus* is considered as a synonym of *G. chapmanianus*.

Representative specimens examined. U.S.A. **Florida:** Braidentown, *Tracy 7102* (BM, NY); Brevard Co., *Fredholm 6207* (SI); dry pine barrens near Jacksonville, *Curtiss 6262* (NY).

6. Gymnopogon delicatulus (C. B. Clarke ex Hook. f.) Bor, Grasses Burma, Ceylon, India & Pakistan 472. 1960. Basionym: *Chloris delicatula* C. B. Clarke ex Hook. f., Fl. Brit. India [J. D. Hooker] 7(22): 290. 1896 [1897]. TYPE: India. Madhya Pradesh: Mandu, Hazarabagh, Chota Nagpore, 18 Oct. 1883, *C. B. Clarke 33855* (lectotype, designated here, K not seen, K photo at SI!). Figure 6.

Plants annual, slender, with 1 to 4 ascendent culms, 13–30 cm, 0.5–1 mm diam., terete, simple or slightly branched; internodes yellowish to brownish, inconspicuously striate, glabrous; nodes slightly narrowed, brown reddish, glabrous; floriferous culms terete, glabrous, inconspicuously striate. Sheaths equal or shorter than the internodes, finely striate, yellowish, glabrous, villous in the margins near the collar; ligules 0.1–0.3 mm, membranous, the margin densely ciliate; pseudoligule a ring of macrohairs up to 2 mm; collar whitish, strongly narrowed, glabrous, with hairs toward the margins; blades linear-lanceolate, 1–3.5 × 0.1–0.3 cm, distichous, divergent on the lower 2/3 of the culms, convolute, subcordate, the apex acuminate, longitudinally striate, glabrous on both surfaces, with scabrous margins. Inflorescence of (6 to)7 to 9(to 12) spiciform racemes, 3–6 cm, ascendent, alternate; main axis triquetrous, 1–2 cm, glabrous, with scabrous angles; rachis of the racemes triquetrous 0.1–0.2 mm wide, straight, violaceous, glabrous, scabrous at the angles, floriferous from the base. Spikelets fusiform, laterally compressed, 1.8–2.2 mm, 1-flowered, tight against the rachis, subsessile, alternate and distant in 2 series along the rachis; pedicels ca. 0.1 mm, flattened, glabrous. Glumes subequal, lower glume 1.8–2 mm, upper glume 2–2.2 mm, longer than the floret, membranous, violaceous, 1-nerved, the nerve scabrous, otherwise glabrous, awnless; floret shortly stipitate, callus ca. 0.2 mm, villous; lemma membranous, ca. 1.4 mm, 3-nerved, the nerves inconspicuous, shortly bifid at the apex, yellowish, with whitish macrohairs 0.1–0.3 mm at the margins and scattered on the base, mainly at the middle nerve, with a straight or slightly flexuous subapical awn, 6–7 mm, violaceous, shortly hispid; palea membranous, pale, 2-nerved, 5–6 mm, shortly laciniate at the apex, slightly pubescent all over the surface; rachilla prolonged behind the floret, terete, ca. 1 mm, scabrous, its apex ending in 2(to 3) awnlike rudiments, 4–7 mm, unequal in length, scabrous. Caryopsis fusiform, 0.7–1 mm; embryo less than 1/3 the length of the caryopsis, hilum basal, punctiform.

Distribution. *Gymnopogon delicatulus* is the single Old World species of the genus, with an annual habit, where it is found in southern Asia, in Burma (Myanmar), India, and Thailand, between 200 and 400 m in elevation. Specimens of this species from Cambodia have been studied by Smith (1971: 359).

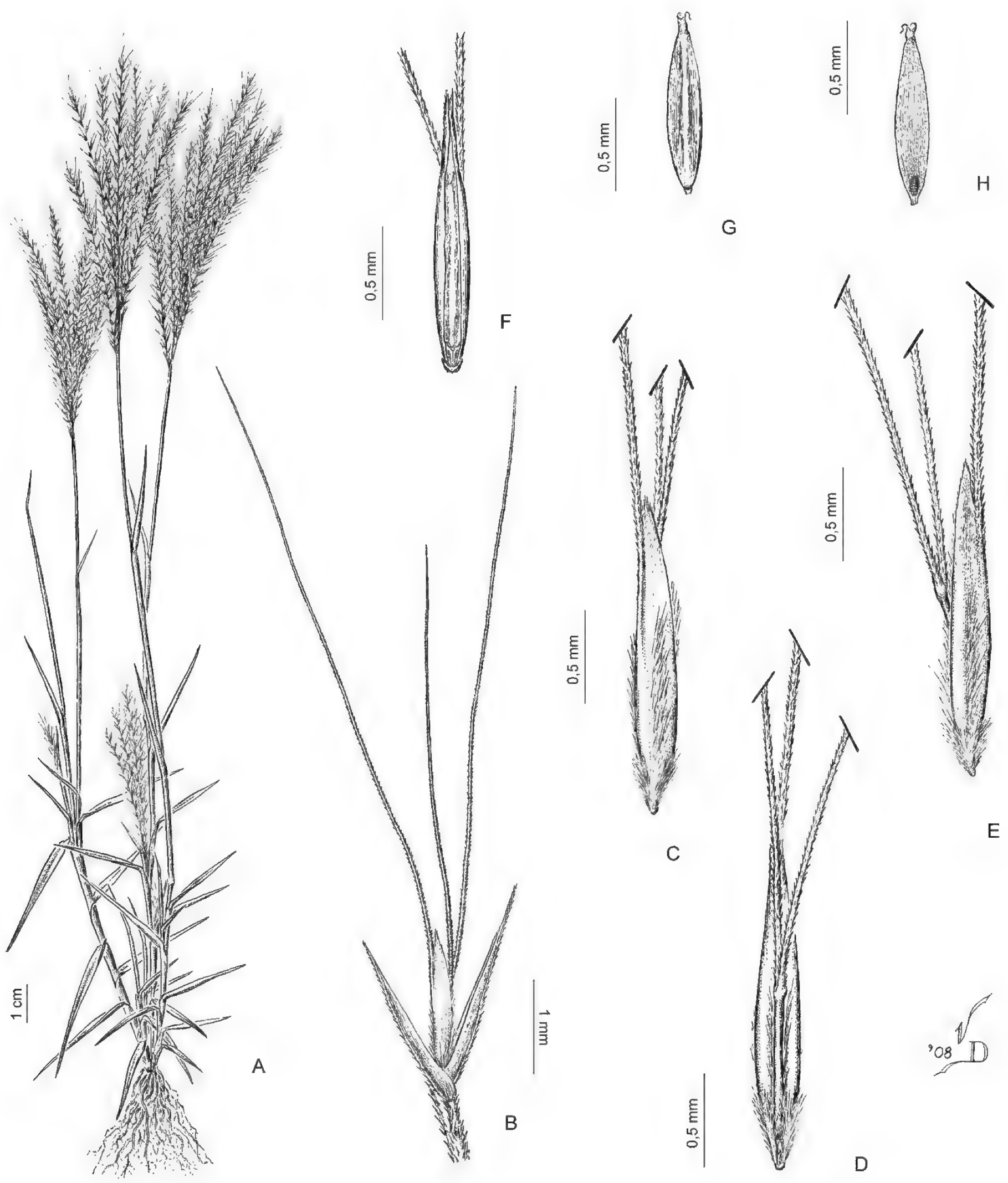

Figure 6. *Gymnopogon delicatulus*. —A. Habit. —B. Spikelet. —C–E. Spikelet detached from glumes, three different views. —F. Palea with lodicules and flower. —G. Caryopis, scutellar view. —H. Caryopsis, hilum view. A–H drawn from *Charoenphol et al. 4934* (NY).

The taxon is noted as flowering between July and November.

Observations. Hooker (1897: 290) mentioned two specimens in the protologue of *Chloris delicatula*: the lectotype (*Clarke 33855*) was collected in India and the specimen *Kurz 1175* is from Pegu-Yoma in Burma (Myanmar). Hooker (1897: 290) mentioned two specimens in the protologue of *Chloris delicatula*, both without collection numbers: the lectotype was collected in India and the second by Kurz, from Pegu-Yoma in Burma (Myanmar). Both syntypes were located at the herbarium of the Royal Botanic Gardens, Kew (K), and a photograph of each was analyzed. Both specimens include drawings with details of spikelet structure. The specimen collected in India is here designated as the lectotype, as it is the one that better matches the protologue.

Gymnopogon delicatulus and *G. foliosus* (Willd.) Nees share the presence of two or three awnlike rudiments at the end of the rachilla. *Gymnopogon foliosus* differs by its robust habit, longer florets 1.6–2.3 mm, with glabrous lemmas, and awns (7–) 8.5–23 mm.

Representative specimens examined. MYANMAR. **Bago:** Pegu Yomah, Herb., *Kurz 1175* (K, syntype). THAILAND. **Chiang Mai:** Doi Suthep, *Kerr 156103* (BM). **Loei:**

Figure 7. *Gymnopogon doellii*. —A′. Habit, basal portion. —A. Habit, apical portion. B. Portion of the rachis with spikelets. —C. Spikelet. —D. Spikelet detached from glumes, lateral view. —E. Spikelet detached from glumes, ventral view. A–E drawn from *Bianchetti & Batista 1516* (CEN); A′ drawn from *Martins s.n.* (CEN-64736).

Na noi, foothill of Phu Kradung, *Charoenphol et al. 4934* (NY).

7. **Gymnopogon doellii** Boechat & Valls, Bradea 5(28): 314. 1990. TYPE: Brazil. Distrito Federal: Area de Proteção ambiental da Bacia do Rio São Bartolomeu, ca. 5 km S do local onde será construida a barragem do futuro lago, em leito seco de um córrego temporário, 6 June 1989, *T. S. Filgueiras & S. P. Araújo 1803* (holotype, CEN not seen; isotypes, CEN-12341 not seen, CEN photo at SI!, IBGE not seen). Figure 7.

Gymnopogon rigidus Döll, Fl. Bras. (Martius) 2(3): 80. 1878, nom. illeg., non *Gymnopogon rigidus* Thwaites, Enum. Pl. Zeyl. [Thwaites]: 372. 1864. TYPE: Brazil. Minas Gerais: "Habitat ad Lagoa Santa Prov. Minarum," *J. E. B. Warming s.n.* (holotype, B not seen).

Plants perennial, rhizomatous, rhizomes ca. 1 cm, short and thick; culms 50–100 cm, 2.5–6 mm diam., robust, rigid, simple, ascendent; internodes yellowish, somewhat brownish near the nodes, finely striate, glabrous; nodes slightly thickened, brownish, glabrous; floriferous culms terete or angular, glabrous. Sheaths longer than the internodes, striate, brownish, glabrous, the margins smooth, densely villous toward the collar; ligules ca. 0.2 mm, membranous, the margin irregular and shortly ciliate; pseudoligule absent; collar conspicuous, brownish, strongly narrowed, villous toward the margin, otherwise glabrous; blades broadly lanceolate, 5–9 × 0.7–1.7 cm, distichous, ascendent or divergent, flat, subcordate, acute or acuminate, longitudinally striate on both surfaces, adaxial surface glabrous, abaxial surface puberulous, the margins scabrous. Inflorescence of 15 to 30 spiciform racemes, 9–21 cm, robust, exserted or partially included in the upper sheath, divergent, alternate; main axis triquetrous, 13–14 cm, glabrous; rachis of the racemes 0.2–0.3 mm wide, straight, brownish, densely villous at the base, otherwise glabrous, with scabrous angles, floriferous from the base, with basal spikelets developed. Spikelets fusiform, laterally compressed, 5.1–9.6 mm, 1-flowered, tight against the rachis, alternate in 2 series along the rachis, imbricate at the apex, shortly pedicellate; pedicels 1.5–2 mm, flattened, puberulent. Glumes subequal, lower glume 5.1–9 mm, upper glume 5.2–9.6 mm, conspicuously longer than the floret, membranous, yellowish, 1-nerved, slightly indurated, awnless, scabrous along the nerve, glabrous on the rest of the surface; floret shortly stipitate, callus near 0.3 mm, blunt, subglabrous; lemma membranous, 2.4–3.1 mm, 3-nerved, the nerves conspicuous, minutely bifid at the apex, yellowish, with few macrohairs near the margins at the apex and all over the surface, with a subapical awn 7–12 mm, straight, scabrous; palea membranous, pale, 2-nerved, 2–2.9 mm, scabrous on the nerves and near the apex, otherwise glabrous; rachilla prolonged behind the floret, terete, 1–1.5 mm, scabrous, the apex ending in a reduced floret, with lemma 0.5–1.2 mm, villous toward the margins and apex, with an awn 2.2–7 mm. Caryopsis fusiform, ca. 2.3 mm, brownish; embryo less than 1/3 the length of the caryopsis, hilum basal, punctiform.

Distribution and habitat. *Gymnopogon doellii* has been rarely found in Brazil, collected from the states of Minas Gerais, Goiás (according to Boechat & Valls, 1990a: 314, 1990b: 12), and Distrito Federal, and is noted as flowering between February and June.

Observations. *Gymnopogon doellii* has spikelets with conspicuous, acuminate glumes that are twice the length of the fertile floret. The presence of this long acumen makes the spikelets imbricate at the apex of the spiciform racemes. *Gymnopogon doellii* is similar to *G. spicatus* in habit and size, the latter species differing by having a pseudoligular ring of hairs, and by its inflorescences with glumes shortly aristulate. *Gymnopogon doellii* is also related to *G. ambiguus*, the latter with shorter glumes 4–5.5 mm, not conspicuously acuminate, and lemmas 3–4 mm, often longer than the 2.4–3.1 mm lemmas seen in *G. doellii*.

Representative specimens examined. BRAZIL. **Distrito Federal:** Brasília, Faz. Sucupira, campo sujo à esquerda da mata do Riacho Fundo, *Bianchetti & Batista 1516* (CEN); Parque Nac. de Brasília, transição entre a cascalheira do entroncamento e o cerrado, May 2007, *Martins s.n.* (CEN 64736).

8. **Gymnopogon fastigiatus** Nees, Fl. Bras. Enum. Pl. 2: 430. 1829. *Monochaete fastigiata* (Nees) Döll, Fl. Bras. (Martius) 2(3): 79. 1878. *Doellochloa fastigiata* (Nees) Kuntze, Revis. Gen. Pl. 2: 773. 1891. TYPE: Brazil. São Paulo: "[h]abitat in campis altis, Generales dictis, provinciae S. Pauli," *Martius s.n.* (holotype, B 100367066 image!; isotype, LE-TRIN-2119.01 fragm. ex B!). Figure 8.

Plants perennial, slightly caespitose, rhizomatous, rhizomes 1–1.2 cm, short and thick, from which several culms generally develop; culms (35–)40–90(–120) cm, ca. 0.5 mm diam., ascendent, simple, occasionally branched and geniculate at the basal nodes; internodes yellowish or brownish, inconspicuously striate, glabrous; nodes inconspicuous, yel-

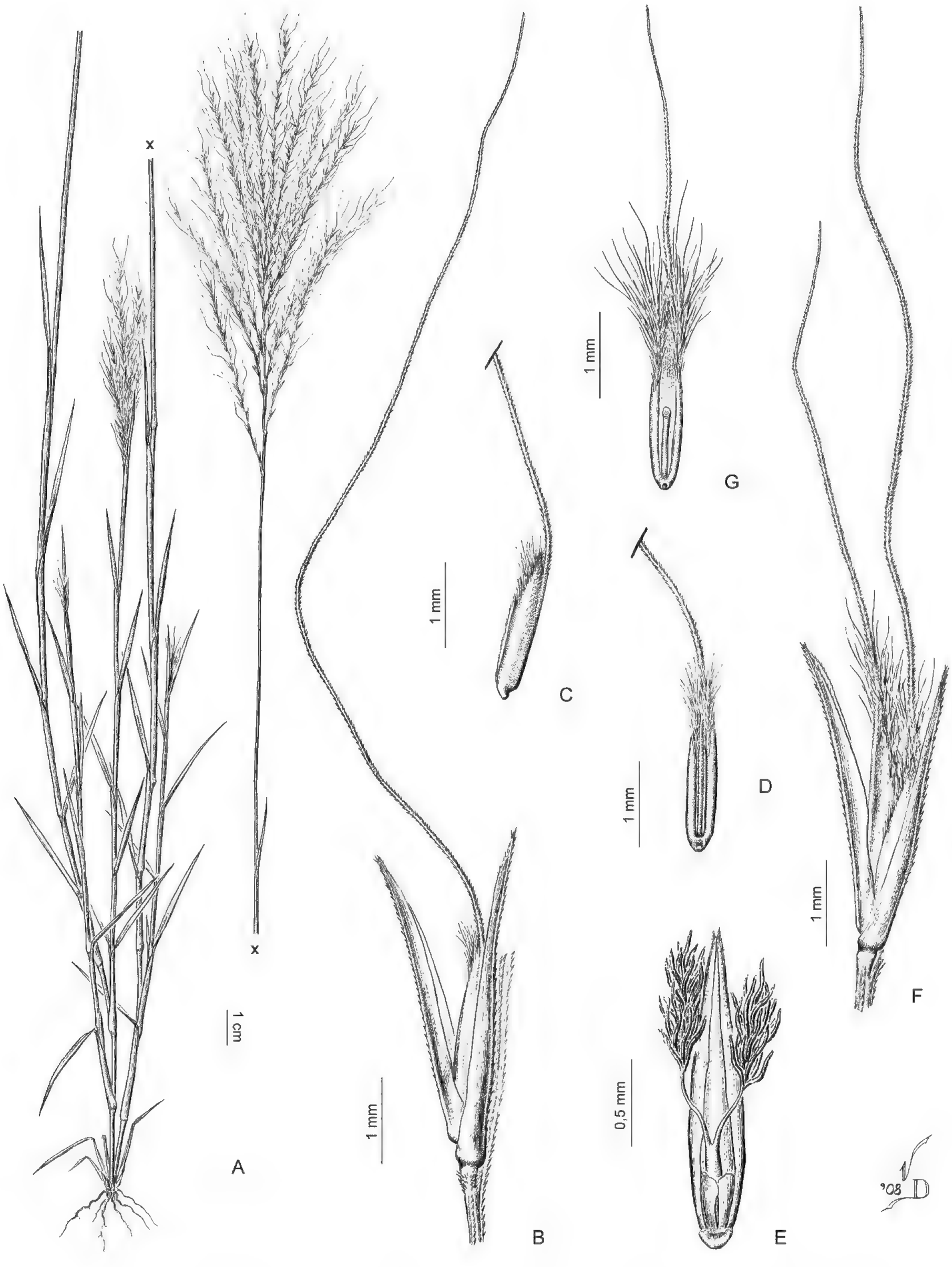

Figure 8. A–E. *Gymnopogon fastigiatus* subsp. *fastigiatus*. —A. Habit. —B. Spikelet. —C. Floret, lateral view. —D. Floret, ventral view. —E. Palea, lodicules, and stigmas. F, G. *Gymnopogon fastigiatus* subsp. *jubiflorus*. —F. Spikelet. —G. Floret. A–E drawn from *Irwin 16429* (NY); F, G drawn from *Killeen 2588* (NY).

lowish, glabrous; floriferous culms terete, yellowish, inconspicuously striate, glabrous or scabrous. Sheaths shorter or longer than the internodes, striate, yellowish, glabrous, the margins smooth; ligules 0.1–0.3 mm, membranous, the margins densely ciliate; pseudoligule, when present, a group of long macrohairs near the margins of the ligule; collar conspicuous, reddish, strongly narrowed, glabrous; blades linear-lanceolate, (1.5–)2.5–4.5(–10.5) × 0.1–0.3(–0.4) mm, distichous, ascendent or divergent, convolute, slightly subcordate at the base, acuminate, longitudinally striate on both surfaces, adaxial surface hispidulous, abaxial surface glabrous, the margins scabrous. Inflorescence of (3 to)4 to 20 spiciform racemes (2–)6–9 cm, ascendent, alternate; main axis triquetrous 4.5–6.5 cm, longitudinally

sulcate, brownish, scabrous at the angles, otherwise glabrous; rachis of the racemes nearly 0.2 mm wide, sinuous, greenish, hispidulous over the entire surface, mainly at the angles, floriferous from the base, with spikelets developed basally. Spikelets fusiform, laterally compressed, 3.5–4.5 mm, 1- to 2-flowered, tight against the rachis, subsessile, alternate and distant in 2 series along the rachis; pedicels 0.3–0.5 mm, terete, hispidulous. Glumes subequal, lower glume 3.5–4 mm, upper glume 3–4.5 mm, longer than the florets, membranous, violaceous, 1-nerved, the nerve conspicuous, greenish and scabrous, slightly indurated, outwardly curved to straight, glabrous, awnless; lower floret shortly stipitate, callus 0.1–0.2 mm, blunt, glabrous; lemma membranous, 1.8–2 mm, 3-nerved, the nerves inconspicuous, minutely bifid and laciniate at the apex, yellowish, glabrous all over the surface, with dense whitish macrohairs (0.3–)1.5–2 mm on the distal third of the margins, with a subapical awn 8–14 mm, slightly bigeniculate and twisted along its length except on the base, violaceous, scabrous; palea membranous, pale, 2-nerved, equal to the lemma, shortly laciniate at the apex, glabrous; rachilla prolonged behind the floret, terete, ca. 1.4–1.5 mm, glabrous to hispidulous, the apex ending in an awnlike rudiment up to 0.5 mm, scabrous. Caryopsis fusiform, ca. 1.5 mm (immature), brownish.

Observations. Hitchcock (1927) mentioned the similarity between *Gymnopogon fastigiatus* and *G. jubiflorus*, and gave a list of characters to identify them, mainly related to spikelet characters. Smith (1971), after studying material of both species, including the type material of *G. jubiflorus*, considered that this species should be recognized as a subspecies, as *G. fastigiatus* subsp. *jubiflorus* (Hitchc.) J. P. Smith. He used only reproductive characters to distinguish them: subspecies *fastigiatus* has, according to Smith (1971: 361), spikelets 1-flowered, lemmas shortly pubescent, and glumes not outwardly curved, while subspecies *jubiflorus* has spikelets 2-flowered, lemmas with longer hairs, and glumes curved. Boechat and Valls (1990b) also considered *G. jubiflorus* as a synonym of *G. fastigiatus*.

Within the specimens examined here, the presence of 2-flowered spikelets and long hairs in the lemma (*Beck 2039*, *Killeen 2588*, *Killeen 2077*, all from Bolivia) correspond with *Gymnopogon fastigiatus* subsp. *jubiflorus*, while the 1-flowered spikelets and shorter hairs on the lemma correspond with the autonymic subspecies in the remaining specimens from Brazil, Colombia, and Venezuela, as well as collections from Bolivia. Smith's concept (1971) is followed in the present contribution; nevertheless, the shape of the glumes is variable, ranging from outwardly curved to straight, and is not considered of sufficient taxonomic value to distinguish both taxa at the species level.

KEY TO THE SUBSPECIES OF *GYMNOPOGON FASTIGIATUS*

1a. One floret; lemma with hairs 0.3–1 mm..... ..... 8a. *G. fastigiatus* subsp. *fastigiatus*
1b. Two florets; lemma with hairs 1.5–2 mm..... ..... 8b. *G. fastigiatus* subsp. *jubiflorus*

8a. Gymnopogon fastigiatus subsp. **fastigiatus.**

Distribution and habitat. *Gymnopogon fastigiatus* subsp. *fastigiatus* has been collected from Colombia, Venezuela, Brazil, and Bolivia. It is present in open, humid fields between sea level and 600 m, flowering between December and July.

Representative specimens examined. BOLIVIA. **Santa Cruz:** Nuflo de Chavez, Est. San Josecito, 8 km NW of Concepción, 16°05′S 62°05′W, *Killeen 1029* (NY). BRAZIL. **Santa Catarina:** Barra do Garças-Xavantina rd., 25 km from Xavantina, *Hunt 5905* (NY). COLOMBIA. **Vichada:** ca. 8 km E of Las Gaviotas along dirt rd. to Santa Rita, *Davidse & Llanos 5179a* (NY). VENEZUELA. **Amazonas:** Atures, pequeña sabana ubicada entre los cerros al N de Laguna Maguari, vertientes SE del valle del Alto Río Parucito, 5°43′N 65°48′W, *Huber 4576* (NY); Rio Puciari tributary of Rio Ituxi, 20 km above mouth, *Prance et al. 13816* (NY). **Bolívar:** W base of Cerro Marimarota, ca. 5 km upstream from mouth, *Wurdack & Monachino 41113* (NY).

8b. Gymnopogon fastigiatus subsp. **jubiflorus** (Hitchc.) J. P. Smith, Iowa State J. Sci. 45: 361. 1971. Basionym: *Gymnopogon jubiflorus* Hitchc., Contr. U.S. Natl. Herb. 24(8): 412. 1927. TYPE: Bolivia. La Paz: Guanay, N Bolivia, 600 m, May 1886, *H. H. Rusby 215* (holotype, US-879400!, US photo at SI!).

Distribution and habitat. *Gymnopogon fastigiatus* subsp. *jubiflorus* has been collected in northern and eastern Bolivia, between 200 and 500 m elevation. Flowering was noted between May and July.

Representative specimens examined. BOLIVIA. **Beni:** Yacuma, Est. Porvenir, Est. Biológica del Beni, 14°35′S 66°30′W, *Killeen 2588* (NY). **Santa Cruz:** Ñuflo de Chavez, Est. John Sandiforth, 5 km S of Concepción, 16°10′S 62°0′W, *Killeen 2077* (NY).

9. Gymnopogon foliosus (Willd.) Nees, Fl. Bras. Enum. Pl. 2: 426. 1829. Basionym: *Chloris foliosa* Willd., Sp. Pl. ed. 4 [Willdenow] 4: 924. 1806. *Biatherium foliosum* (Willd.) Desv., Mém.

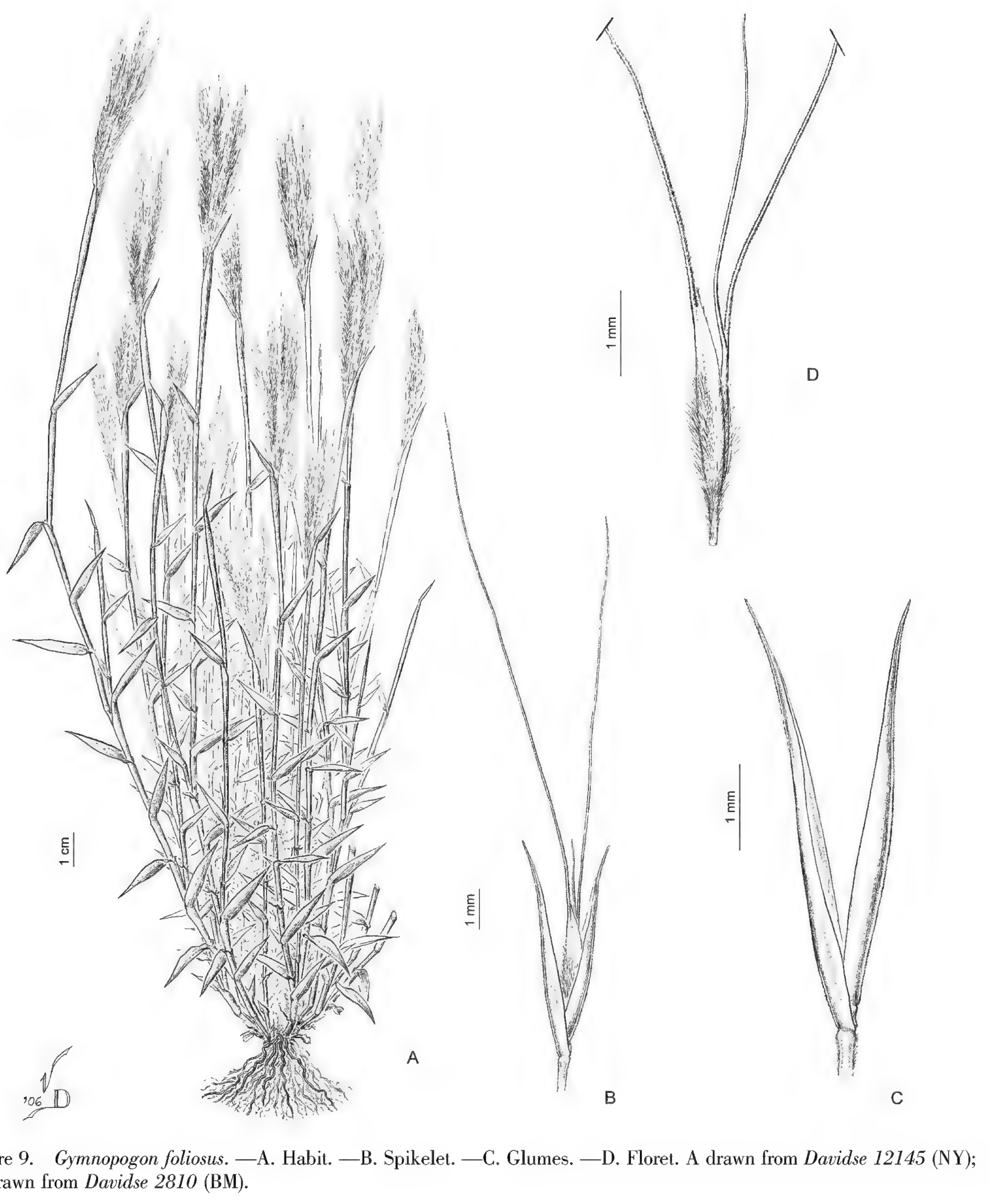

Figure 9. *Gymnopogon foliosus*. —A. Habit. —B. Spikelet. —C. Glumes. —D. Floret. A drawn from *Davidse 12145* (NY); B–D drawn from *Davidse 2810* (BM).

Soc. Agric. Angers 1: 176. 1831. TYPE: Virgin Islands: "Habitat in insula St. Thomas Americes (v.s.)," *E. P. Ventenat s.n.* (holotype, B, B photo at SI!; isotypes, BM!, US fragm. ex B not seen). Figure 9.

Aristida geminata Willd. ex Steud., Nomencl. Bot. [Steudel], ed. 2, 1: 131. 1840, nom. inval., pro syn. *Gymnopogon foliosus* (Willd.) Nees.

Chloris aristida Salzm. ex Steud., Syn. Pl. Glumac. 1: 218. 1854, nom. inval., pro syn. *Gymnopogon foliosus* (Willd.) Nees.

Aristida chloris Salzm. ex Döll, Fl. Bras. (Martius) 2(3): 83. 1878, nom. nud.

Gymnopogon pullulans Döll, Fl. Bras. (Martius) 2(3): 82. 1878. TYPE: Brazil. S. loc., s.d., *W. J. Burchell 5398* (lectotype, designated by Smith [1971: 366], K not seen, K photo at SI!; duplicates, B image!, GH!, P not seen).

Plants annual, slightly caespitose; culms 15–50(–75) cm, 0.5–0.6 mm diam., ascendent, simple and erect or branched and geniculate at the basal nodes; internodes yellowish, finely striate, slightly thickened toward the nodes, glabrous; nodes inconspicuous, brownish, glabrous; floriferous culms terete, yellowish, longitudinally striate, glabrous. Basal sheaths longer than the internodes, the upper ones shorter, finely striate, yellowish, glabrous, the

margins shortly hispid to densely villous near the collar; ligules 0.1–0.5 mm, membranous, the margin densely ciliate; pseudoligule a few macrohairs near 1 mm; collar conspicuous, darker than the sheath, strongly narrowed, with few macrohairs; blades lanceolate, 8–15(–37) × 0.1–0.3 cm, distichous, divergent, convolute, occasionally flat, subcordate at the base, acute, longitudinally striate and glabrous on both surfaces, the margins hispidulous. Inflorescence of (2 to)4 or 5(to 10) spiciform racemes 2.5–4(–5.5) cm, partially included in the upper sheath, ascendent or divergent, digitate or subdigitate; main axis 1–2 cm, longitudinally sulcate, yellowish, scabrous at the angles, otherwise glabrous; rachis of the racemes nearly 0.2 mm wide, straight, yellowish, the angles greenish, hispidulous over the entire surface, floriferous from the base. Spikelets fusiform, laterally compressed, (3–)4.5–5.5(–7) mm, 1(to 2)-flowered, tight against the rachis, subsessile, densely alternate in 2 series along the rachis; pedicels ca. 0.5 mm, flattened, hispid. Glumes subequal, lower glume (2.5–)4.5–6 mm, upper glume (2.5–)4.5–5.5(–7) mm, longer than the florets, membranous, yellowish to violaceous, 1-nerved, the nerve conspicuous, yellowish and scabrous, slightly indurated, glabrous, awnless; floret shortly stipitate, callus near 0.8 mm, thin, hispid; lemma membranous, 1.6–2.3 mm, 3-nerved, the lateral nerves inconspicuous, shortly bifid at the apex, violaceous, glabrous, with a subapical awn (7–)8.5–23 mm, straight or slightly geniculate, yellowish or violaceous, hispidulous; palea membranous, pale, 2-nerved, equal to the lemma, glabrous; rachilla prolonged behind the floret, terete, near 1 mm, glabrous, the apex ending in 2 awnlike rudiments 3.8–15 mm, unequal in length, straight to slightly geniculate, shortly hispidulous. Caryopsis fusiform, near 1.2 mm, brownish red, glabrous; embryo less than 1/3 the length of the caryopsis, hilum basal, punctiform.

Distribution and habitat. *Gymnopogon foliosus* is distributed from the Caribbean (Puerto Rico, Virgin Islands, St. Thomas) through northern South America (Venezuela, Guyana, French Guiana, Suriname, and Brazil). It grows in sandy or stony soils up to 1200 m and is a typical species of cerrados and savannas.

Observations. Moscoso (1943) and Urban (1920) cited this species in Hispaniola, while Boechat and Valls (1990b) cited it in Colombia.

Representative specimens examined. BRAZIL. **Amapá:** Rio Araguari, 2 km from river, along rd. from Porto Platon to Macapa, *Pires et al. 51064* (NY). **Amazonas:** Estr. Terra Preta, Km 2, branch of Manaos Manacapuri 5 km from Cacau Pirêra, *Prance 23530* (NY). **Bahia:** Rio Roda Velha, ca. 150 km SW of Barreiras, *Irwin et al. 14933* (NY). **Distrito Federal:** Brasília, s.d., *Riedel s.n.* (SI 26007); Brasília, *Irwin et al. 15315* (NY). **Goiás:** 10 km SW of Alvorada do Norte along hwy. BR-020, *Davidse et al. 12200* (NY). **Maranhão:** Loreto, ca. 25 km S of city of Loreto, 7°17′S 45°7–8′W, *Eiten & Eiten 4159* (NY). **Mato Grosso:** Serra do Roncador, Río Turvo, ca. 210 km N of Xavantina, *Irwin et al. 16072* (NY). **Minas Gerais:** Diamantina, Fondo do Matador, *Mexía 5853a* (BM); Serra do Cabral, Joaquim Felício, *Hatschbach 64845* (CTES). **Pará:** Itaituba, estr. Santarém-Cuiabá, BR 163, Km 794, Serra do Cachimbo, *Amaral et al. 991* (NY). **Paraíba:** Cerrados, près de João Pessoa, *Schnell 9489* (SI). **Pernambuco:** Cururú, *Rosa & Santos 1870* (NY). **Rondônia:** BR-364, entre Pimenta Bueno e Vilhena, *Seitz s.n.* [ICN 23745] (CTES). **Roraima:** 10 km NNW of Bôa Vista on BR 174, mtn. ca. 1 km E of rd., *Coradin & Cordeiro 759* (NY). **São Paulo:** Itirapina, Rod. São Paulo-São Carlos, 10 km E da cidade de Itirapina, 22°16′00″S, 47°44′30″W, *Mimura 354 D* (NY). COLOMBIA. S. loc., *Linden 1564* (BM). FRENCH GUIANA. Iracoubo, *Hoock 1151* (NY). GUYANA. Wismar, *Hitchcock 17273* (BM, NY); Meribisci Lake, *Jenman 2246* (BM); Rupunini, *Jenman 5993* (BM, NY). PUERTO RICO. Near Laguna Tortuguero, *Britton & Britton 7955* (NY). SURINAME. Sipaliwini savanna 5 km W of Morro Grande, *Oldenburger et al. 431* (NY). VENEZUELA. **Amazonas:** Atures, alrededores de Puerto Ayacucho, 30 km N Sabanas de Rincones de Chacorro, a 5 km al NE de Galipero, 5°48′ N 67°20′W, *Huber 4770* (NY). **Anzoátegui:** 18 km W of El Tigra rd. to Pariaguán, on Mesa Guanipa, *Davidse et al. 4973* (MO, NY). **Bolívar:** Piar, Uriman, 5°21′N 62°37′W, *Davidse & Huber 23119* (MO, NY). **Zulia:** vic. of Mene Grande, *Pittier 10599* (NY).

10. Gymnopogon glaber Caro, Dominguezia 5: 17. 1982. TYPE: Argentina. Salta: Dpto. Anta, Cerro Maldonado, June 1934, *A. Ragonese 131* (holotype, BA!; isotype, BAA!). Figure 10.

Plants perennial, rhizomatous, rhizomes long and thin, stoloniform, from which several aerial shoots develop; culms terete, 15–40 cm, 0.8–1 mm diam., ascendent, generally branched at the basal nodes; internodes yellowish or brownish, finely striate, glabrous; nodes yellowish to brownish, slightly thickened, glabrous; floriferous culms terete, yellowish, longitudinally striate, hispid at the apex, otherwise glabrous. Sheaths longer than the internodes, finely striate, pale at the margins, glabrous; ligules 0.2–0.3 mm, membranous, the margin densely ciliate; pseudoligule absent; collar conspicuous, yellowish or reddish, strongly narrowed, glabrous; blades lanceolate, 4.5–7 × 0.5–0.6 cm, distichous, divergent, flat, slightly subcordate at the base, acute, longitudinally striate and glabrous on both surfaces, the margins scabrous. Inflorescence of 6 to 9 spiciform racemes 8–13 cm, divergent; main axis 4–6 cm, longitudinally sulcate, yellowish, scabrous at the angles, otherwise glabrous; rachis of the racemes near 0.2 mm wide, straight, yellowish, the angles hispidulous, without spikelets at the proximal portion. Spikelets fusiform, laterally compressed, 3–4.5 mm, 1-flowered, tight against the rachis, subsessile, alternate

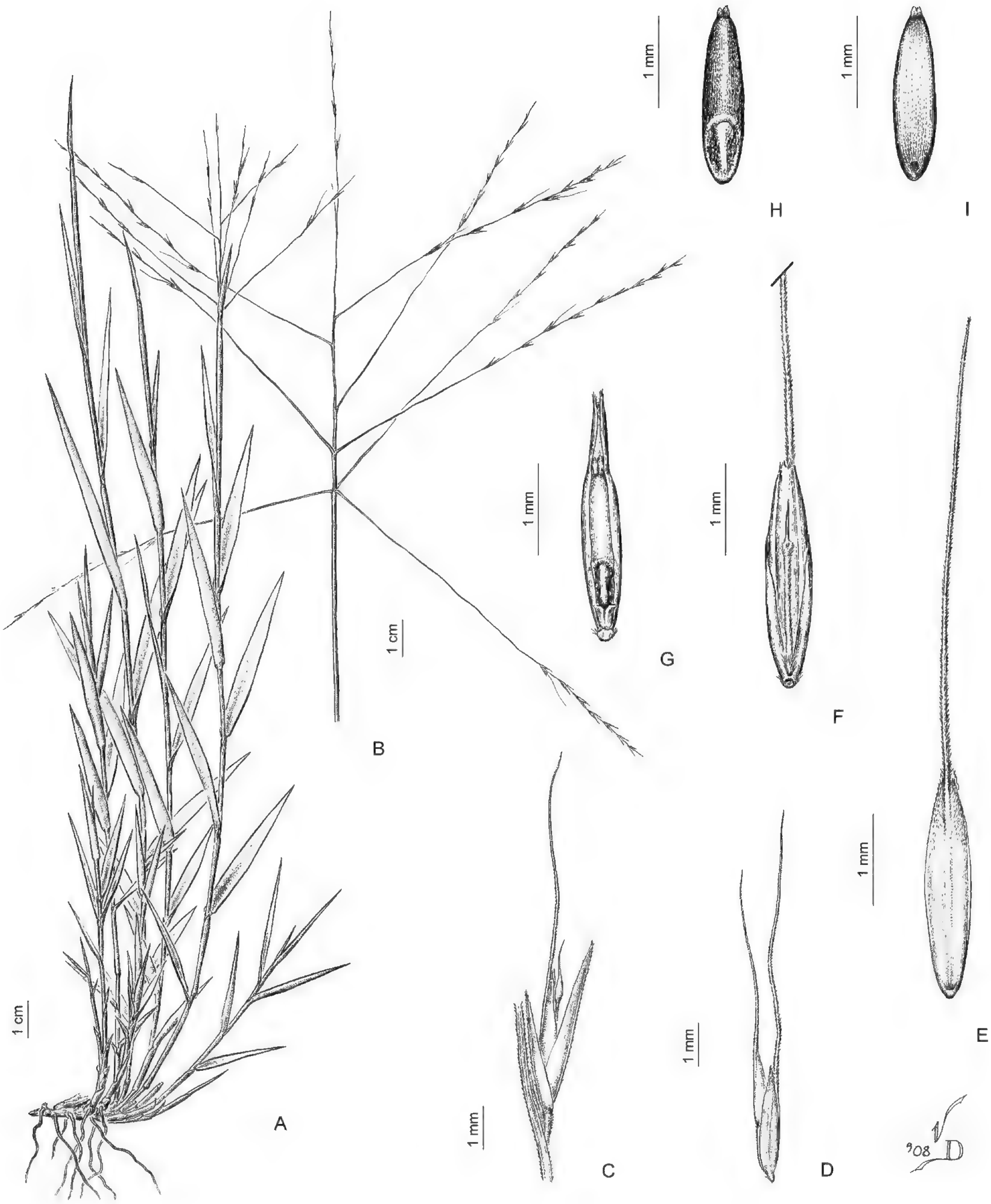

Figure 10. *Gymnopogon glaber*. —A. Habit. —B. Inflorescence. —C. Portion of the rachis with a spikelet. —D. Spikelet detached from glumes. —E. Floret, dorsal view. —F. Floret, ventral view. —G. Palea with lodicules and caryopsis. —H. Caryopsis, scutellar view. —I. Caryopsis, hilum view. A–I drawn from *A. Ragonese 131* (BA).

and distant in 2 series along the rachis; pedicels ca. 0.5–1 mm, slightly angular, hispid. Glumes subequal, lower glume 3–3.5 mm, upper glume 4–4.5 mm, longer than the florets, membranous, yellowish, glabrous, 1-nerved, the nerve conspicuous, greenish and scabrous, awnless; floret shortly stipitate, callus near 0.2 mm, thin, villous; lemma membranous, 2–3 mm, 3-nerved, the lateral nerves inconspicuous, shortly bifid at the apex, yellowish, glabrous, with a subapical awn 5–7 mm, straight or slightly curved, yellowish or violaceous, scabrous; palea membranous, pale, 2-nerved, equal to the lemma, glabrous, scabrous on the nerves; rachilla prolonged behind the floret, terete, near 1 mm, glabrous, the apex ending in an awnlike rudiment ca. 1.5 mm, occasionally this rudiment also consisting of an infertile lemma. Caryopsis fusiform, near 2 mm, brownish, glabrous; embryo less than 1/3 the length of the caryopsis, hilum basal, punctiform.

Distribution and habitat. *Gymnopogon glaber* has been collected in northern Argentina, in the provinces of Jujuy, Salta, Tucumán, and Catamarca, in margins of forests between 1300 and 1800 m. The

taxon has been noted as flowering between February and April.

Observations. *Gymnopogon glaber* is morphologically similar to *G. grandiflorus*, the latter species having lemmas usually pubescent toward the base (vs. glabrous in *G. glaber*) and bigger florets (3.8–4.8 mm in *G. grandiflorus* vs. 2.5–3.5 mm in *G. glaber*).

Representative specimens examined. ARGENTINA. **Catamarca:** Ambato, camino de Singuil-Balcosna, 10 km E del cruce de rutas, Sierra de Graciana, *Saravia Toledo et al. 13308* (CTES, NY). **Jujuy:** Dr. Manuel Belgrano, camino a Tiraxi, ruta prov. 29, *Zuloaga et al. 8658* (SI). **Salta:** Guachipas, ruta nac. 9, Pampa Grande, *A. Hunziker 1679* (BAA, CORD). **Tucumán:** Tafí, Siambón, *Díaz 9601* (BAA); Siambón, *Olea 64 a* (BAA).

11. Gymnopogon grandiflorus Roseng., B. R. Arrill. & Izag., Bol. Fac. Agron. Univ. Montevideo 103: 20. 1968. TYPE: Uruguay. Dpto. Maldonado: Arroyo Solís, próx. a la barra, 8 Apr. 1955, *B. Rosengurtt B-6347* (holotype, MVFA not seen, MVFA photo at SI!; isotype, BAA!, BAA photo at US-2946505!). Figure 11.

Gymnopogon spicatus (Spreng.) Kuntze var. *brevisetus* Hack., Anales Mus. Nac. Buenos Aires 21 (ser. 3, 14): 117. 1911. *Gymnopogon brevisetus* (Hack.) J. P. Smith, Iowa State J. Sci. 45(3): 344. 1971. TYPE: Argentina. Buenos Aires: Est. Santa Rita, por Vela, 16 Apr. 1908, *T. Stuckert 18744* (holotype, G not seen, G photo at SI!).

Plants perennial, rhizomatous, rhizomes short, occasionally long and stoloniform, from which several aerial shoots develop; culms terete, 25–45(–60) cm, 0.5–1.2 mm diam., slender, ascendent or decumbent, generally simple, rarely branched, erect to slightly geniculate at the basal nodes; internodes yellowish, finely striate, glabrous; nodes inconspicuous, slightly thickened or compressed, glabrous; floriferous culms terete, yellowish, longitudinally striate and hispid at the apex, otherwise glabrous. Sheaths longer than the internodes, finely striate, yellowish, pale toward the margins, glabrous; ligules ca. 0.5 mm, membranous, the margin densely ciliate; pseudoligule absent; collar conspicuous, yellowish to reddish, strongly narrowed, glabrous; blades lanceolate, 5–8(–10) × 0.3–0.5 cm, distichous, ascendent, flat, subcordate at the base, acute, longitudinally striate and glabrous on both surfaces, the margins hispid and slightly involute at the apex. Inflorescence of 6 to 13 spiciform racemes 10–15 cm, partially included in the upper sheath, divergent; main axis (3–)5–9 cm, longitudinally sulcate, yellowish, scabrous at the angles, otherwise glabrous; rachis of the racemes 0.1–0.3 mm wide, slightly sinuous, yellowish green, the angles hispidulous, otherwise glabrous, without spikelets at the proximal portion. Spikelets fusiform, laterally compressed, 3.5–5.5 mm, 1- or 2-flowered, tight against the rachis, subsessile, alternate and distant in 2 series along the rachis; pedicels ca. 0.5 mm, terete, hispid. Glumes subequal, lower glume 3.5–5 mm, upper glume 4.5–5.5 mm, longer than the florets, membranous, violaceous, glabrous, 1-nerved, the nerve conspicuous, yellowish and scabrous, otherwise glabrous, with margins scabrous, awnless; lower floret shortly stipitate, callus near 0.8 mm, thin, hispid; lemma membranous, 3.5–4(–5.5) mm, 3-nerved, the nerves inconspicuous, shortly bifid and laciniate at the apex, yellowish, glabrous, usually pubescent basally, with a subapical awn 5.5–9(–12) mm, straight or slightly geniculate, yellowish or violaceous, hispid; palea membranous, pale, 2-nerved, equal to the lemma, minutely laciniate at the apex, glabrous; rachilla prolonged behind the floret, terete, near 1 mm, scabrous, the apex ending in an awnlike rudiment 0.8–3 mm, scabrous. Caryopsis fusiform 2.4–3 mm, brownish or violaceous; embryo less than 1/3 the length of the caryopsis, hilum basal, punctiform.

Distribution and habitat. *Gymnopogon grandiflorus* grows in Uruguay, Brazil, and Argentina, and Smith (1971) cited this species for Peru. It grows in open fields on sandy or clay soils and has been reported to flower between February and May.

Observations. The specimens *Swallen 9201* and *9235* (NY), collected in Rio Grande do Sul, Brazil, have florets 3–3.5 mm, smaller than those typically seen in *Gymnopogon grandiflorus*, with the lemma lacking the basal pubescence and completely glabrous, characters that place both specimens near *G. glaber*. However, the latter species has even smaller florets, 2–2.5 mm, and has been collected only from northern Argentina to date.

Within the specimens examined, a gradation in lemma pubescence could be observed, from glabrous to villous in different portions. *Gymnopogon grandiflorus* is morphologically similar to *G. glaber* (see observation under the latter species).

Representative specimens examined. ARGENTINA. **Buenos Aires:** Saavedra, Sierra Currumalán, 20 Mar. 1918, *Hauman s.n.* (BAA 5338). **Córdoba:** Calamuchita, Los Reartes, *Sayago 3075* (BAA). **Entre Rios:** Gualeguaychú, Paranacito, *Martínez Crovetto 5019* (BAB). BRAZIL. **Rio Grande do Sul:** Bagé, *Swallen 9049* (NY). URUGUAY. **Florida:** Campo Exp. de pastos, Ea. Rincón de Santa Elena, *Gallinal & Rosengurtt PE-6034* (BAA, SI).

12. Gymnopogon legrandii Roseng., B. R. Arrill. & Izag., Bol. Fac. Agron. Univ. Montevideo 103: 22. 1968. TYPE: Uruguay. Canelones: Carrasco,

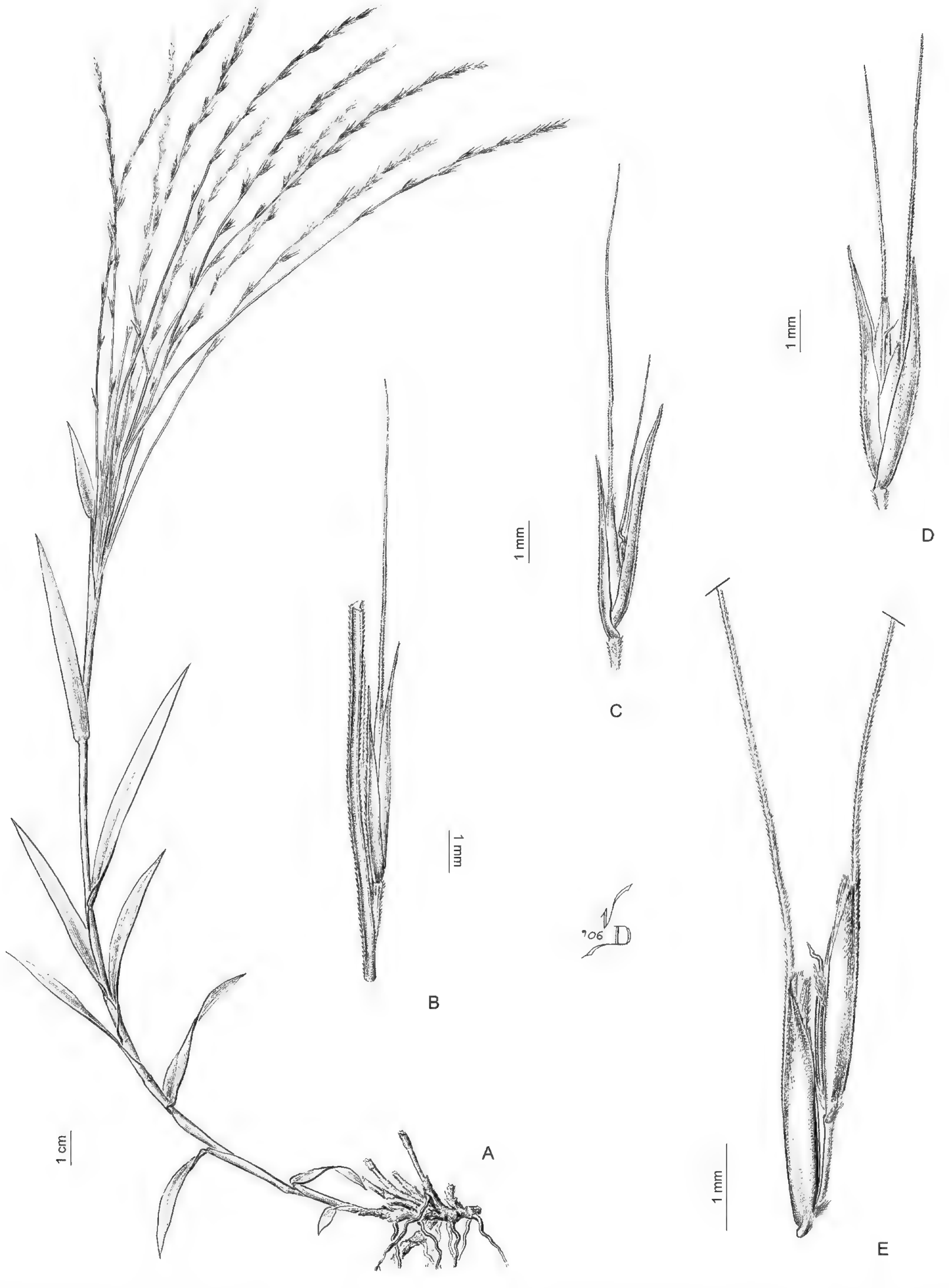

Figure 11. *Gymnopogon grandiflorus*. —A. Habit. —B. Portion of the rachis with a 1-flowered spikelet. —C, D. Two-flowered spikelets from the proximal floriferous portion of the rachis and the distal portion of it, respectively. —E. Two-flowered spikelet detached from glumes. A–E drawn from *Venturi 10245* (NY).

Aeropuerto, en arenas, 4 Mar. 1949, *B. Rosengurtt B-5291* (holotype, MVFA not seen, MVFA photo at SI!; isotypes, BAA-1386!, SI!, US not seen). Figure 12.

Gymnopogon biflorus Pilg. var. *ciliatilemma* Burkart, Bol. Soc. Argent. Bot. 12: 290. 1968. TYPE: Argentina. Entre Ríos: Dpto. Gualeguaychú, predelta, Ibicuy, 4 Dec. 1930, *A. Burkart 3598* (holotype, SI!; isotype, SI!).

Gymnopogon swallenii J. P. Smith, Iowa State J. Sci. 45(3): 373. 1971. TYPE: Brazil. Rio Grande do Sul: Rio Grande, 3 May 1946, *J. R. Swallen 9235* (holotype, US-1960896 not seen, US photo at SI!; isotype, US-3135306 not seen, US photo at SI!).

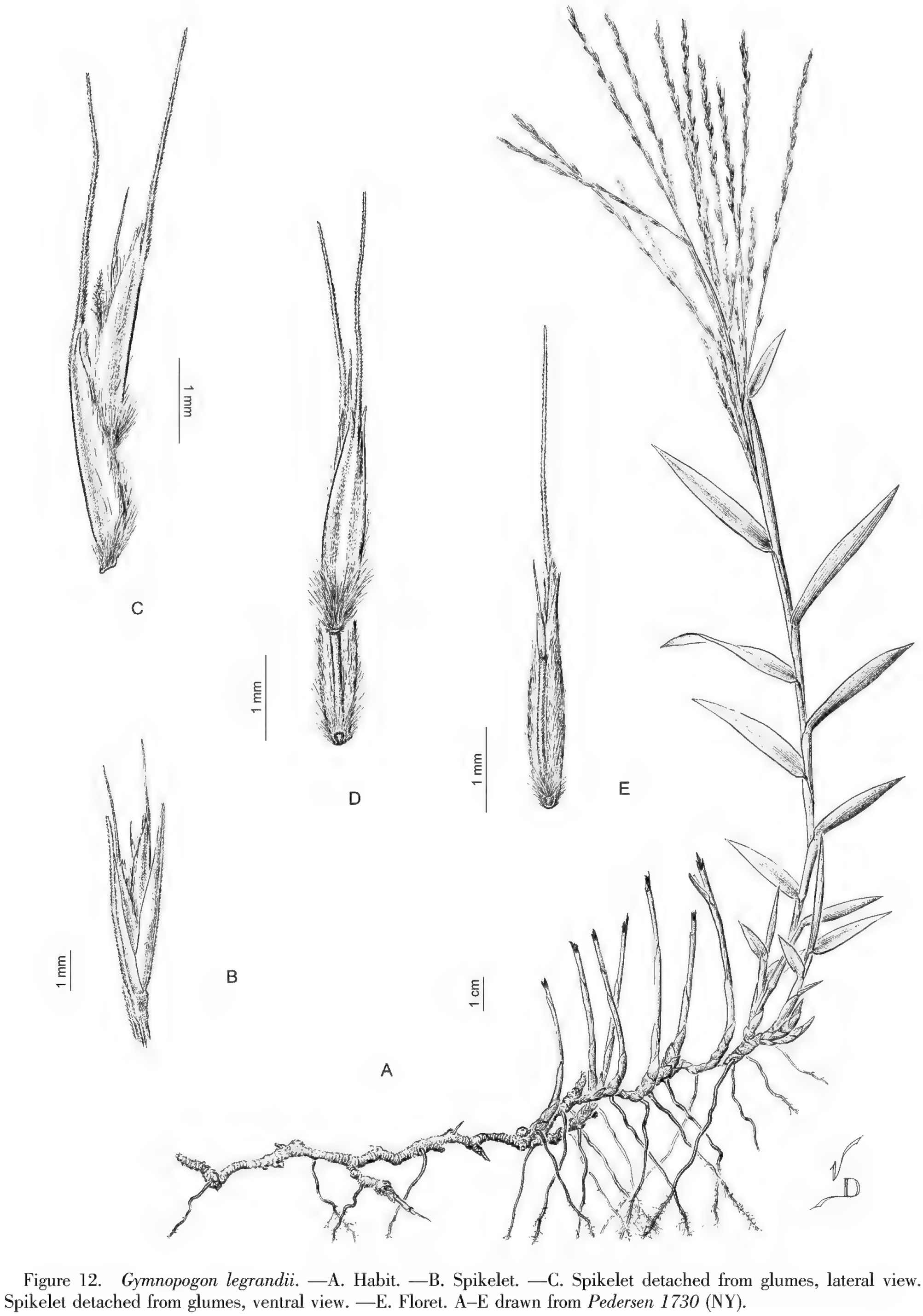

Figure 12. *Gymnopogon legrandii*. —A. Habit. —B. Spikelet. —C. Spikelet detached from glumes, lateral view. —D. Spikelet detached from glumes, ventral view. —E. Floret. A–E drawn from *Pedersen 1730* (NY).

Plants perennial, rhizomatous, rhizomes stoloniform, thin (2–3 mm diam.), yellowish, glabrous, from which several aerial shoots develop; culms terete, 30–60 cm, slender, ascendent or decumbent, simple, erect; internodes yellowish, inconspicuously striate, glabrous; nodes inconspicuous, slightly thickened, yellowish, glabrous; floriferous culms terete, yellowish, longitudinally striate and hispid at the apex, otherwise glabrous. Sheaths longer than the internodes, finely striate, yellowish, pale toward the

margins, glabrous; ligules 0.6–0.8 mm, membranous, the margin densely ciliate; pseudoligule absent; collar inconspicuous, whitish to reddish, strongly narrowed, glabrous, occasionally villous at the margins; blades oblong-lanceolate, 2.6–5(–10) × 0.2–0.6 cm, distichous, ascendent or divergent, flat, subcordate at the base, acute, longitudinally striate and glabrous on both surfaces, rarely somewhat hispid, the margins hispid and slightly involute at the apex. Inflorescence of 4 to 14 spiciform racemes (7–) 10–17(–19) cm, divergent, violaceous; main axis 10–12 cm, longitudinally sulcate, yellowish, scabrous at the angles, otherwise glabrous; rachis of the racemes 0.3–0.8 mm wide, straight, yellow greenish, the angles hispidulous, with hairs all over the surface near the base, otherwise glabrous, with reduced spikelets at the base. Spikelets fusiform, laterally compressed, 3–6 mm, 1- or 2-flowered, tight against the rachis, subsessile, alternate and distant in 2 series along the rachis; pedicels ca. 0.3–0.8 mm, terete, slightly flattened, scabrous. Glumes subequal, lower glume 3–5 mm, upper glume 4–6 mm, longer than the florets, membranous, yellowish tinged with violet, glabrous, 1-nerved, the nerve conspicuous, yellowish and scabrous, otherwise glabrous, with margins scabrous, awnless; lower floret shortly stipitate, callus near 0.2 mm, thick, densely villous; lower floret with lemma membranous, 2.5–3 mm, 3-nerved, the nerves inconspicuous, shortly bifid at the apex, violaceous at the base, otherwise yellowish, villous toward the margins and the base, glabrous on the rest of the surface, with a subapical awn 3–3.5(–7) mm, straight, yellowish, hispid; palea membranous, pale, 2-nerved, equal to the lemma, minutely laciniate at the apex, glabrous; upper floret when present similar to the lower one but smaller; rachilla prolonged behind the floret, terete, near 1 mm, scabrous, the apex ending in an awnlike rudiment 1–2.5 mm, scabrous. Caryopsis fusiform 2–2.2 mm, brownish; embryo less than 1/3 the length of the caryopsis, hilum basal, punctiform.

Distribution and habitat. *Gymnopogon legrandii* has been collected in Brazil, Uruguay, and Argentina, in open, sandy soils and in flower between November and May.

Observation. *Gymnopogon legrandii* is clearly differentiated from the rest of the species of the genus by a combination of two unique characters: by the presence of long stoloniform rhizomes and by having reduced spikelets at the base of the spiciform racemes.

Representative specimens examined. ARGENTINA. **Córdoba:** Punilla, Sierra Grande, falda E, ca. de la entrada a la Ea. San Bernardo, *A. Hunziker 12038* (BAA, CORD). **Corrientes:** Goya, ruta 12, 40 km S de Goya, *Krapovickas et al. 27255* (CTES). **Entre Ríos:** Gualeguaychú, de Ceibas a Médanos, *Troncoso et al. 3248* (SI); Gualeguaychú, Holt, *Martínez Crovetto 2191* (SI). **Misiones:** San Ignacio, campo antes de la entrada al Parque Prov. Teyucuaré, 27°16′S 55°33′W, *Zuloaga et al. 5747* (SI).

13. Gymnopogon spicatus (Spreng.) Kuntze, Revis. Gen. Pl. 3(3): 354. 1898. Basionym: *Polypogon spicatus* Spreng., Syst. Veg. (ed. 16) [Sprengel] 1: 243. 1824. *Trichochloa spicata* (Spreng.) Schult., Mant. 3 (Schultes & Schultes f.): 577. 1827. *Muhlenbergia spicata* (Spreng.) Kunth, Révis. Gramin. 1: 64. 1829. TYPE: Brazil. S. loc., s.d., *F. Sellow s.n.* (holotype, B not seen; isotype, B fragm. at BAA!, B fragm. at US not seen). Figure 13.

Gymnopogon biflorus Pilg., Bot. Jahrb. Syst. 30(1): 139–140. 1901. TYPE: Brazil. Mato Grosso: "auf trocknem, steinigen Boden im Oberen Cuyabathal," Apr. 1899, *H. Meyer 489* (holotype, B not seen; isotype, B fragm. at BAA!).

Gymnopogon laevis Nees, Fl. Bras. Enum. Pl. 2(1): 428. 1829. TYPE: [Uruguay]. "Habitat ad Monte Video," s.d., *F. Sellow s.n.* (holotype, B not seen; isotypes, L-12088 not seen, B fragm. at US!).

Gymnopogon laevis Nees var. *pluriflorus* Döll, Fl. Bras. (Martius) 2(3): 81. 1878. *Gymnopogon spicatus* (Spreng.) Kuntze var. *pluriflorus* (Döll) Stuck., Anales Mus. Nac. Buenos Aires 21: 117. 1911. *Gymnopogon spicatus* var. *pluriflorus* (Döll) Parodi, Physis (Buenos Aires) 4: 174. 1918, nom. illeg. *Gymnopogon spicatus* (Spreng.) Kuntze var. *pluriflorus* (Döll) Rojas, Revista Jard. Bot. Mus. Hist. Nat. Paraguay 2: 170. 1923, nom. superfl. TYPE: Brazil. "Prope Ypanema," s.d., *J. G. F. Riedel s.n.* (holotype, W not seen).

Gymnopogon filiformis Griseb., Fl. Brit. W.I. [Grisebach] 538. 1864. TYPE: Trinidad. S. loc., s.d., *Crueger s.n.* (holotype, GOET not seen; isotypes, B not seen, US-822349 photo at SI!).

Gymnopogon spicatus (Spreng.) Kuntze var. *longiaristatus* Kuntze, Revis. Gen. Pl. 1: 354. 1891. *Gymnopogon spicatus* (Spreng.) Kuntze f. *longiaristatus* (Kuntze) J. P. Smith, Iowa State J. Sci. 45(3): 371. 1971. TYPE: Bolivia. Ost-Velasco, 200 m, July 1892, *O. Kuntze s.n.* (lectotype, designated by Smith [1971: 372], NY not seen, NY photo at SI!).

Plants caespitose, perennial, rhizomatous, rhizomes thickened and short, yellowish, glabrous, from which several aerial shoots develop; culms terete, 30–100 cm, 1–2 mm diam., ascendent or decumbent, simple or branched, erect; internodes yellowish to brownish, inconspicuously striate, glabrous; nodes inconspicuous, slightly thickened, yellowish, glabrous; floriferous culms terete, yellowish, longitudinally striate and hispid at the apex, otherwise glabrous. Sheaths shorter than the internodes, finely striate, yellowish, generally villous toward the margins and collar, otherwise glabrous;

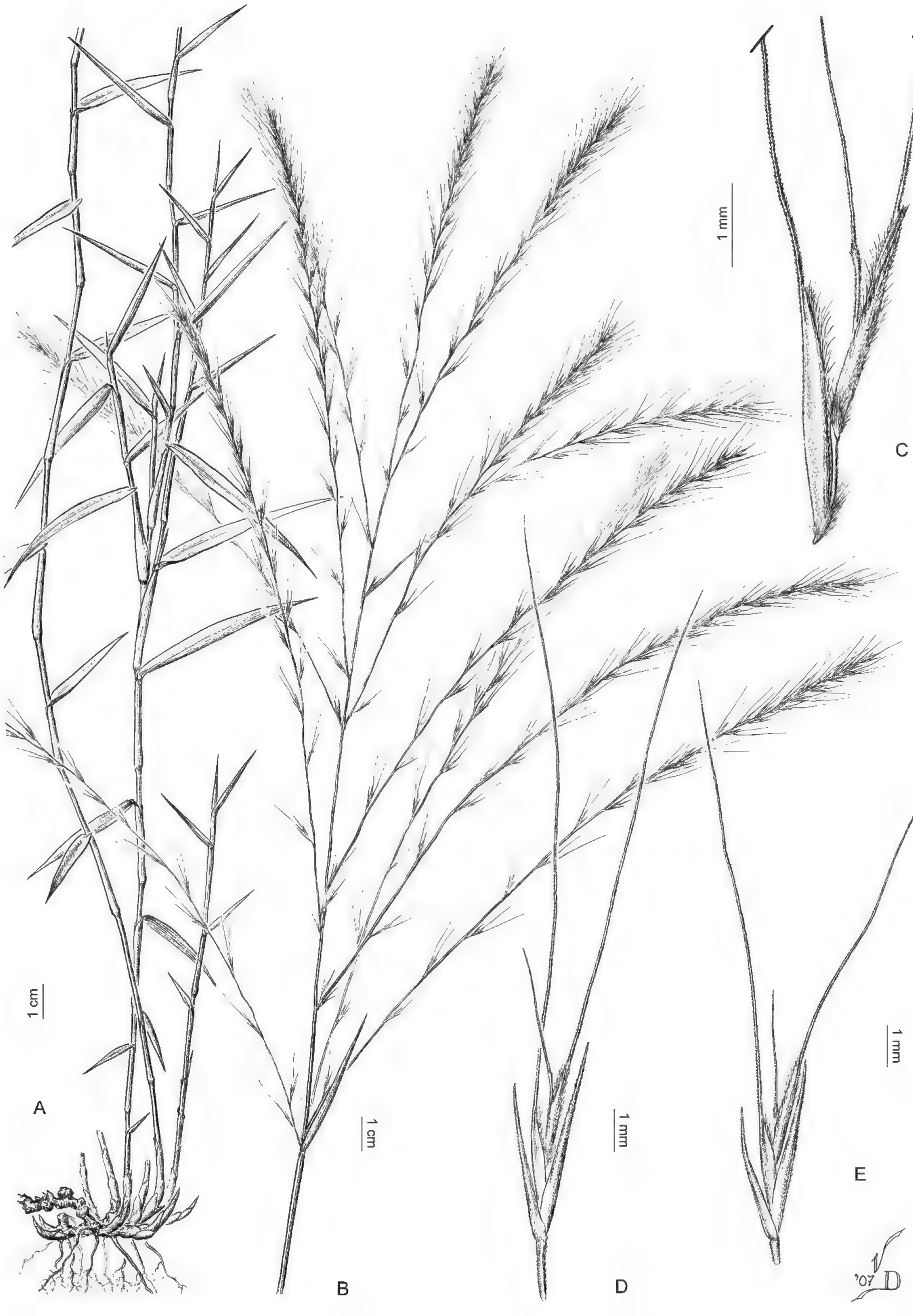

Figure 13. *Gymnopogon spicatus*. —A. Habit. —B. Inflorescence. —C. Spikelet without glumes. —D, E. Two-flowered spikelets from the proximal floriferous portion of the rachis and the distal portion of it, respectively. A–E drawn from *Killeen 2481* (SI).

ligules 0.1–0.4 mm, membranous, the margin densely ciliate; pseudoligule a ring of hairs ca. 2 mm; collar conspicuous, yellowish, strongly narrowed, densely villous, sometimes only villous at the margins; blades broadly lanceolate, (1.5–)2.8–6(–9) × 0.2–1.2 cm, distichous, ascendent or divergent, flat or convolute, rigid, subcordate or truncated at the base, acuminate, longitudinally striate and glabrous on both surfaces, with scabrous margins. Inflorescence of 6 to 35 spiciform racemes 4.5–33 cm, ascendent or divergent; main axis 9–16 cm, longitudinally sulcate, yellowish, scabrous at the

angles, otherwise glabrous; rachis of the racemes 0.2–0.3 mm wide, straight, yellowish, the angles pilose, otherwise glabrous, floriferous from the base, generally with reduced and distant spikelets at the proximal portion and developed spikelets conspicuously dense at the distal part of the rachis. Spikelets fusiform, laterally compressed, (2.5–)3–8.4 mm, 1- or 2(to 3)-flowered, tight against the rachis, shortly pedicellate, alternate or opposite at the apex in 2 series along the rachis; pedicels 1–1.2 mm, slightly flattened, scabrous. Glumes subequal, lower glume (2.5–)3–7.5 mm, upper glume 3.5–8.4 mm, longer than the florets, membranous, yellowish, glabrous, 1-nerved, the nerve prolonged in an awnlike acumen 0.5–2.5(–3) mm, scabrous, on both or one of the glumes; lower floret subsessile, callus obliquely truncate, pubescent; lemma membranous, 2.2–4 mm, 3-nerved, the nerves inconspicuous, with white hairs 0.2–1 mm on the surface and margins, occasionally glabrous, shortly bifid at the apex, with a subapical awn (4–)9–15(–30) mm, straight or slightly curved, yellowish, hispid; palea membranous, pale, 2-nerved, 2–3 mm, minutely laciniate at the apex, pubescent on the surface and margins; upper floret similar to the lower one but smaller; rachilla prolonged behind the floret, terete, 0.5–2 mm, scabrous, the apex ending in an awnlike rudiment 2–5(–7) mm, scabrous. Caryopsis fusiform, 1–2.4 mm, brownish; embryo less than 1/3 the length of the caryopsis, hilum basal, punctiform.

Distribution and habitat. *Gymnopogon spicatus* is distributed in the southern United States, in Mexico, Belize, and Guatemala in Mesoamerica, and in Colombia, Venezuela, Brazil, Bolivia, Peru, Paraguay, Uruguay, and Argentina in South America. The species has been collected from sea level to 2300 m, with flowering noted between December and June.

Observations. Smith (1971) placed *Gymnopogon biflorus* under the synonymy of *G. spicatus* and mentioned the presence of conspicuously acuminate glumes, but not awned, for this species; he also mentioned that *G. aristiglumis* is the only species of the genus that has awned glumes. Caro (1982), in his revision of the Argentinean species of *Gymnopogon*, considered *G. spicatus* and *G. biflorus* as separate, valid species, both with glumes attenuated into awns; he distinguished them by the number of fertile florets within the spikelets and the indument of the lemma. For *G. spicatus*, Boechat and Valls (1990b) described the presence of awns 0.5–3.5(–5.5) mm on one or both glumes, but they did not consider this character to identify the taxon in the key to species of Brazil. In the present contribution, *G. spicatus* and *G. aristiglumis* are both considered with awned glumes, although in *G. spicatus* the awn is short, 0.5–2.5(–3) mm, and is better considered as an awnlike acumen (see observation under *G. aristiglumis*). *Gymnopogon spicatus* is one of the most frequently encountered species of the genus in Central and South America. However, it is of little economic value, probably due to its rigid blades. This is a variable species, regarding reproductive characters of the spikelets, such as the number of florets, the length of the glumes and lemmas, and the length of the awns. This variation led the authors to recognize varieties or forms within the species, which are here placed under synonymy.

Representative specimens examined. ARGENTINA. **Chaco:** 1ro. De Mayo, Colonia Benítez, *Schulz 3213* (CTES, SI). **Córdoba:** Calamuchita, Valle de los Reartes, *Castellanos 3361* (BAA). **Corrientes:** Bella Vista, barrancas arenosas del río Paraná, *Boelcke 1596* (BAA, SI). **Entre Ríos:** Concordia, Est. Agronómica, *Burkart 910* (BAA). **Formosa:** Patiño, Estanislao del Campo, *Schulz 13975* (BAA, CTES). **Jujuy:** S. loc., *Parodi 9785* (BAA). **Misiones:** San Ignacio, *Quiroga 793* (BAA). **Salta:** Santa Victoria, Los Toldos, ladera E del Cerro, *Meyer et al. 20585* (BAA). **San Luis:** Pringles, Loma Alta, entre Santo Domingo y Paso del Rey, *Anderson 3534* (CORD). **Tucumán:** Trancas, *Venturi 6761* (NY). BELIZE. All Pines, *Schipp 787* (BM, NY). BOLIVIA. **Chuquisaca:** Azurduy, on ascent above Tarvita to Cerro Viscachani on rd. to Azurduy, *Wood & Serrano 14470* (LPB). **Santa Cruz:** Andrés Ibañez, Viru-Viru Int. Airport, SW of bldgs., *Nee 44332* (NY). **Tarija:** José María Aviléz, Antigal, *Beck 27309* (LPB). BRAZIL. **Bahia:** wet campo, Rio Piau, ca. 150 km SW of Barreiras, *Irwin et al. 14750* (NY). **Distrito Federal:** 31 km from Brasília on Anapolis rd., *Clayton 4817* (NY). **Goiás:** Corumbá de Goiás, GO-Serra dos Pirineus, 10 km NW Cocalzinho, *Burman & Filgueiras 407* (NY). **Mato Grosso:** Nova Andradina, Casa Branca, *Hatschbach 31872* (NY). **Mato Grosso do Sul:** Bonito, terr. of Ponta Porã, *Swallen 9514* (NY); Campo Grande, *Chase 10827* (NY). **Minas Gerais:** Ouro Preto (Villa Rica), *Chase 9357* (NY). **Paraíba:** near João Pessoa, along Rte. BR-101, *Tsugaru & Sano B-1310* (NY). **Paraná:** 12 km SW of Jaguariaíva along hwy. PR-11 to Ponta Grossa, *Davidse et al. 11381* (NY). **Rio Grande do Norte:** Paul dos Ferros, Sítio Mororó, *Santino de Assis & Sarmento 388* (NY). **Rio Grande do Sul:** Pelotas, *da Costa Sacco 102* (BAA). **São Paulo:** Casa Branca, *Chase 10587* (BAA). COLOMBIA. **Magdalena:** Santa Marta, *H. H. Smith 189* (BM, NY). **Tolima:** Honda, *Pennell 3650* (NY). GUATEMALA. **Izabal:** Los Amates, *Weatherwax 1753* (BM). MEXICO. **Veracruz:** Azueta, *Archer 3955* (BM). PARAGUAY. **Alto Paraguay:** San Salvador, *Rojas 2767* (SI). **Amambay:** Cabecera Aquidabán, *Rojas 6615* (BAA); Parque Nac. Cerro Corá, camino lateral entre la Ruta 5 y el área de admin., *Morrone & Pensiero 442* (SI). **Boquerón:** Puerto Sastre, *Ramírez 16* (SI). **Central:** Villeta, Alemán Cué, *Rosengurtt B-5548* (BAA). **Cordillera:** 3 km camino a Paraguarí, *Morrone & Pensiero 109* (SI). **Paraguarí:** Caapucú, Barrerito, *Rosengurtt B-5614* (BAA). **Presidente Hayes:** Gran Chaco, Santa Elisa, *Hassler 2696* (BM, NY).

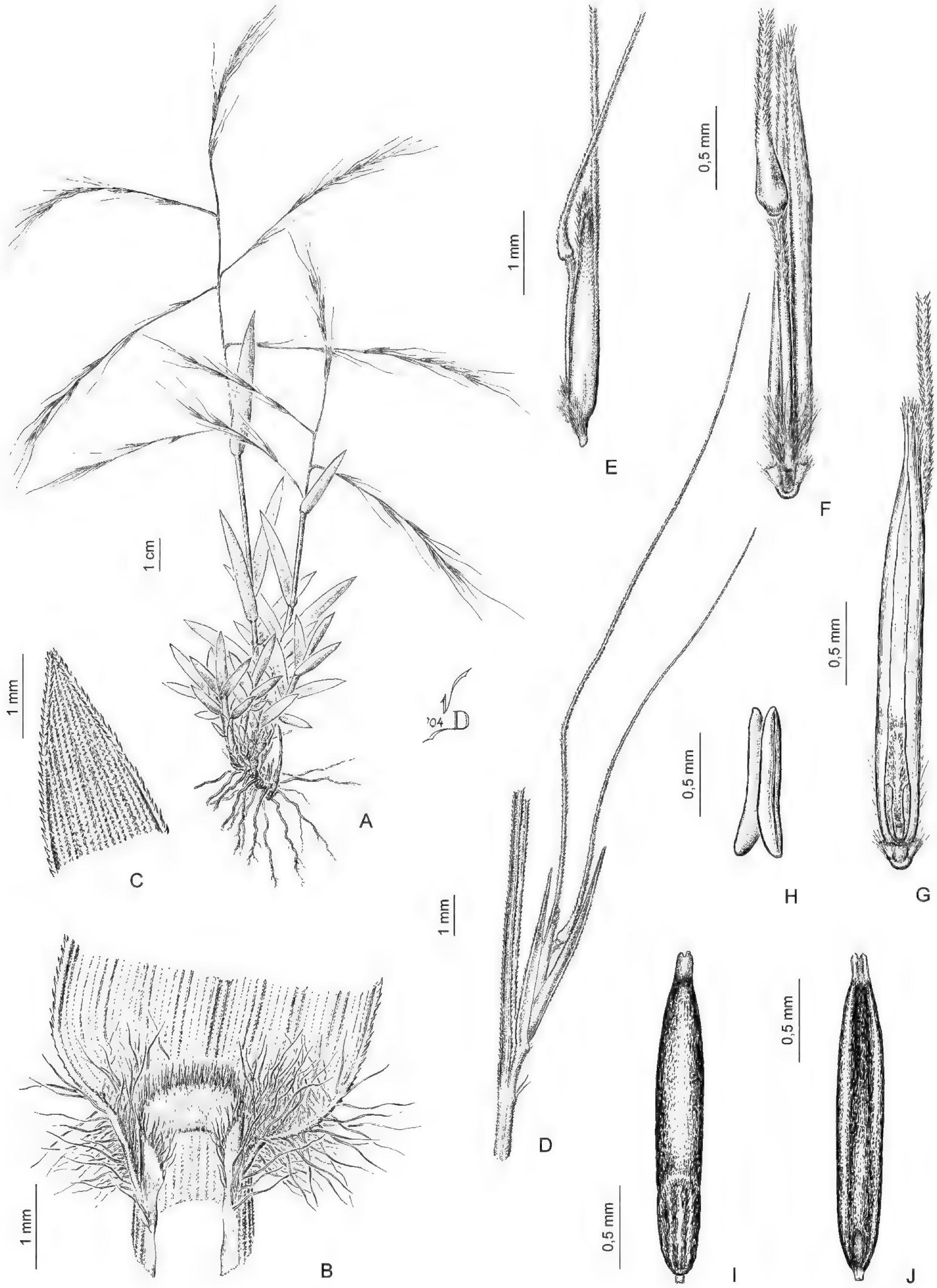

Figure 14. *Gymnopogon toldensis*. —A. Habit. —B. Ligule. —C. Blade apex. —D. Portion of the rachis with one spikelet. —E. Floret, lateral view. —F. Floret, ventral view. —G. Floret, ventral view detached from rachilla. —H. Stamen. —I. Caryopsis, scutellar view. —J. Caryopsis, hilum view. A–J drawn from *Sulekic et al. 810* (SI).

San Pedro: San Estanislao, Jan. 1946, *Bridarolli s.n.* (SI). PERU. **Lambayeque:** Sapotal, *Llatas Quiroz 684* (NY). URUGUAY. **Colonia:** Nueva Palmira, Río Uruguay, *Morrone et al. 5228* (SI). VENEZUELA. **Lara:** Barquisimeto, Loma de León, *Burkart 17128* (SI). **Miranda:** path from Petare to La Guayrita, *Alston 5487* (BM, NY). **Monagas:** sabanas de Cachipo, *Tamayo 3566* (SI). **Trujillo:** Sabana de Monay, *Burkart 16843* (SI).

14. **Gymnopogon toldensis** Sulekic & Rúgolo, Darwiniana 44(2): 504–507. 2006. TYPE: Argentina. Salta: Depto. Santa Victoria, El

Angosto, 5 km E de Los Toldos, 1600 m, 17 Mar. 1986, *A. Sulekic, L. Novara & G. Neumann 810* (holotype, SI!; isotype, Herb. Sulekic not seen). Figure 14.

Plants perennial, rhizomatous, rhizomes thickened and shorter than 1.5 cm, yellowish, glabrous, from which several aerial shoots develop; culms terete, (5–) 15–25 cm, 3–4 mm diam., slender, ascendent, simple, erect; internodes yellowish, inconspicuously striate, glabrous; nodes inconspicuous, slightly thickened, brownish, glabrous; floriferous culms terete, yellowish, longitudinally striate and hispid at the apex, otherwise glabrous. Sheaths longer than the internodes, finely striate, yellowish, pubescent, the margins densely pilose toward the collar, otherwise glabrous; ligules 0.5–0.8 mm, membranous, the margin densely ciliate; pseudoligule absent; collar inconspicuous, slightly darker, strongly narrowed, with macrohairs up to 2 mm at the margins, otherwise glabrous; blades oblong-lanceolate, (0.8–)2–5.5 × (0.15–)0.3–0.5 cm, distichous, ascendent, flat, convolute at the apex, truncated at the base, acute, longitudinally striate and glabrous on both surfaces, the margins hispid, glabrous. Inflorescence of 5 or 6 spiciform racemes 3–6.5 cm, divergent, yellowish; main axis 2–4 cm, slightly flattened, yellowish, scabrous at the angles, otherwise glabrous; rachis of the racemes 0.3–0.5 mm wide, straight or slightly sinuous, yellowish, the angles hispidulous near the base, otherwise glabrous, without spikelets at the basal 1/4. Spikelets fusiform, laterally compressed, 3–6 mm, 1-flowered, tight against the rachis, subsessile, alternate and distant in 2 series along the rachis; pedicels 0.7–0.8 mm, terete, slightly flattened, scabrous. Glumes subequal, lower glume ca. 3 mm, upper glume 3–6 mm, longer than the florets, membranous, yellowish, glabrous, 1-nerved, the nerve conspicuous, yellowish and scabrous on the nerve, awnless; floret shortly stipitate, callus near 0.2 mm, thick, densely villous; lemma membranous, 2.5–3 mm, 3-nerved, the nerves inconspicuous, shortly bifid at the apex, yellowish, with few hairs toward the margins, with a subapical awn (18–)24–25(–33) mm, straight or geniculate, yellowish, hispid; palea membranous, pale, 2-nerved, equal to the lemma, minutely laciniate at the apex, glabrous; rachilla prolonged behind the floret, terete, 1–1.5 mm, scabrous, the apex ending in an awnlike rudiment 5–15(–18) mm, scabrous. Caryopsis fusiform, ca. 1.8 mm, brownish red; embryo less than 1/3 the length of the caryopsis, hilum basal, punctiform.

Distribution and habitat. *Gymnopogon toldensis* is only known from the type collection in Salta, Argentina, on stony slopes.

Observations. *Gymnopogon toldensis* is related to *G. brevifolius*, *G. grandiflorus*, and *G. glaber*, as they share a lack of spikelets at the base of the branches of the inflorescence; however, the presence of long awns, longer than 18 mm, and ligules 0.5–0.8 mm distinguishes *G. toldensis* from the aforementioned species.

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Appendix 1. Examined material of *Gymnopogon*. Each specimen is cited by the last name of the first collector when there is more than one collector. Species number is indicated between parentheses and corresponds to the list of species.

1. *Gymnopogon ambiguus* (Michx.) Britton, Sterns & Poggenb.
2. *Gymnopogon aristiglumis* Hitchc.
3. *Gymnopogon brevifolius* Trin.
4. *Gymnopogon burchellii* (Munro ex Döll) Ekman
5. *Gymnopogon chapmanianus* Hitchc.
6. *Gymnopogon delicatulus* (C. B. Clarke ex Hook. f.) Bor
7. *Gymnopogon doellii* Boechat & Valls
8. *Gymnopogon fastigiatus* Nees

8a. *Gymnopogon fastigiatus* Nees subsp. *fastigiatus*

8b. *Gymnopogon fastigiatus* Nees subsp. *jubiflorus* (Hitchc.) J. P. Smith

9. *Gymnopogon foliosus* (Willd.) Nees
10. *Gymnopogon glaber* Caro
11. *Gymnopogon grandiflorus* Roseng., B. R. Arrill. & Izag.
12. *Gymnopogon legrandii* Roseng., B. R. Arrill. & Izag.
13. *Gymnopogon spicatus* (Spreng.) Kuntze
14. *Gymnopogon toldensis* Sulekic & Rúgolo

Ahles 36570 (3); *Ahumada 4010* (12); *Allison 9547* (3); *Alston 5487* (13); *Amaral 991* (9); *Anderson 3534* (13), *8251* (9), *9322* (9), *9336* (9), *9701* (9), *9973* (9), *10276* (9), *37075* (9); *Araújo 63* (13), *108* (13); *Arbo 927* (13); *Archer 3955* (13); *Athey 2186* (1).

Ball 80 (1); *Batson Jr. 386* (3); *Beck 2039* (8b), *23469* (13), *24152* (8b), *27309* (13); *Bianchetti 1516* (7); *Biganzoli 26* (13); *Biltmore 475c* (1); *Blake 9748* (1); *Blomquist 10159* (1), *s.n.* (3); *Boelcke 1596* (13); *Bordón 344* (13), *s.n.* (13); *Bridarolli s.n.* (13); *Britton 7955* (9); *Bromquist 238* (3); *Burkart 910* (13), *3598* (12), *16843* (13), *17128* (13), *21637* (13); *Burman 407* (13), *419* (9); *Bush 1340* (1), *7883* (1).

Cabrera 32419 (4); *Calderón 949* (2), *2072* (2); *Canby 290* (3), *14981* (1), *15158* (3), *s.n.* (3); *Carnevali 475* (4), *1076* (4), *3185* (4), *4249* (13), *5529* (13), *5987* (12); *Castellanos 3361* (13); *Chapman s.n.* (3); *Charoenphol 4934* (6); *Chase 8002* (9), *8396* (1), *8762* (4), *9357* (13), *10587* (13), *10827* (13), *10962* (4), *11779* (9), *12004* (9), *12060* (9), *12108* (9), *12206* (1), *s.n.* (9); *Cimbra 140* (13); *Clayton 4817* (13); *Coile 1582* (1); *Commons s.n.* (3); *Coradin 759* (9); *da Costa Sacco 102* (13); *Cowan 4115* (13); *Cristóbal 1123* (13); *Curtiss 3441 p.p.* (1), *3441 p.p.* (5), *3442* (3), *4062* (3), *5246* (5), *6262* (5), *s.n.* (1).

Davidse 2810 (9), *4424* (9), *4928* (9), *4973* (9), *5179a* (8a), *11081* (4), *11381* (13), *12145* (9), *12200* (9), *12233* (9), *22611* (9), *22645* (9), *23119* (9), *23126* (9); *Davis 57* (9); *de La Cruz 1701* (9); *Desvaux s.n.* (9); *Díaz 9601* (10); *Dusén 4120* (13).

Earle s.n. (1), *s.n.* (3); *Eggert s.n.* (1); *Eiten 2697* (9), *4159* (9); *Ekman 701* (4), *H 13538* (1); *Elcoro 576* (9); *Ellendale s.n.* (3).

Fernald 15175 (3); *Fredholm 6207* (5).

Gallinal PE-6034 (11); *Gatingen s.n.* (1), *s.n.* (3); *Gehrt 8308* (9); *Gillespie 752* (9); *Glaziou 20099* (9), *s.n.* (9); *Gleason 531* (9); *Glocker 268* (9); *Godfrey 1597* (1), *8094* (1); *Goodland 332* (9), *401* (9), *842* (9).

H. L. B. 776 (3); *Hale s.n.* (3); *Harley 21759* (9); *Harper 2252* (3), *s.n.* (1); *Hassler 2696* (13), *12900* (13); *Hatschbach 3010* (4), *31872* (13), *64845* (9), *64877* (9); *Hauman s.n.* (11); *Hermann 14997* (1); *Herndon 277* (1); *Hill 15844* (3), *22699* (3), *24537* (3); *Hitchcock 660* (1), *906* (1), *17273* (9); *Hoehne 17548* (13); *Holdridge 1215* (1), *1715* (1); *Holm s.n.* (1); *Hoock 1151* (9); *Hostmann 1003* (9); *Howard 8138* (1); *Huber 4576* (8a), *4770* (9), *10272* (9); *Hunt 5616* (9), *5905* (8a); *Hunziker, A. 1679* (10), *12038* (12), *21195* (10).

Ibarrola 2040 (13), *2388* (12), *2904* (13); *Irwin 13073a* (4), *14118* (13), *14474* (9), *14568* (9), *14750* (13), *14933* (9), *15315* (9), *15940* (8a), *16072* (9), *16429* (8a), *17085* (8a), *17303* (8a), *28355* (9), *34838* (13).

Jardim 3643 (9); *Jenman 2246* (9), *5993* (9); *Jiménez 13477* (4), *14641* (4).

Kearney Jr 5 (1); *Kerr 156103* (6); *Killeen 924* (13), *1029* (8a), *1248* (13), *1567* (13), *1990* (13), *2017* (13), *2039* (8a), *2077* (8b), *2092* (13), *2481* (13), *2588* (8b); *Killip 30070* (9); *Koster C5206-1* (1); *Kral 44183* (3), *69705* (1); *Krapovickas 20907* (13), *27255* (12), *31745* (13), *40798* (4); *Kurz 1175* (6).

Letterman s.n. (1); *Linden 1564* (9); *Liogier 12778* (1); *Lippincott s.n.* (3); *Llatas Quiroz 684* (13); *Long 13590* (3); *Longhi-Wagner 9518* (4); *Lorente 1802* (13).

Maas 3678 (9); *Machado de Campos 205* (13); *Mackenzie 6700* (3), *s.n.* (1); *Martinelli 6914* (9); *Martínez Crovetto 2191* (12), *5019* (11), *10543* (13); *Martins s.n.* (7); *McArdle 424* (1); *McGee 1384* (1); *Mendes Magalhães 19192* (9); *Mexía 5853a* (9); *Meyer 489* (13), *797* (13), *2183* (13), *2294* (4), *20585* (13); *Mimura 354 D* (9); *Morrone 80* (13), *109* (13), *442* (13), *518* (13), *5228* (13); *Mroginski 485* (4); *Murca Pires 52166* (9).

Nee 41102 (8a), *41330* (8a), *44332* (13), *46119* (13); *Nicora 385* (13); *Nuttall s.n.* (1).

Oldenburger 431 (9); *Olea 64 a* (10).

Palmer 8876 (3), *29129* (3), *32740* (1); *Parodi 3643* (13), *4542* (4), *5449* (4), *9785* (13), *12062* (13), *12137* (13), *s.n.* (9); *Pedersen 1730* (12); *Pennell 3650* (13); *Pinto 48/86* (9); *Pires 51064* (9); *Pittier 10599* (9); *Pontious 34* (1); *Potzger 10649* (1); *Prance 13816* (8a), *23530* (9); *Pulle 362* (9).

Quiroga 793 (13).

Ragonese, A. 131 (10), *6747* (4); *Ramírez 16* (13); *Ratter 2080* (9); *Reverchon s.n.* (1), *1146* (1); *Ridley s.n.* (9); *Riedel s.n.* (9); *Rodrigues 4535* (9); *Rojas 2767* (13), *6615* (13), *13174* (4), *13252* (4); *Rosa 1870* (9); *Rosengurtt B-5291* (12), *B-5548* (13), *B-5614* (13), *B-6347* (10); *Rua 515* (13); *Rugel 699* (1).

Santino de Assis 388 (13); *Saravia Toledo 13308* (10); *Sayago 3075* (11); *Schinini 14598* (13), *17497* (12), *36048* (13); *Schipp 787* (13); *Schnell 9489* (9); *Schulz 1055* (4), *3213* (13), *3237* (4), *3844* (4), *11516* (4), *12652* (13), *13975* (13), *17059* (13), *18812* (13); *Seitz s.n.* (9); *Serrano 881* (13); *Small 1030* (5), *9388* (3), *s.n.* (1); *Smith 189* (13), *2474* (1), *2475* (3), *2578* (3), *10530* (4), *12095* (4); *Spruce s.n.* (9); *Steinbach 1932* (13); *Steyermark 59203* (9), *131192* (9); *Stone s.n.* (3); *Stuckert 580* (13), *2644* (13), *14164* (13), *18744* (10); *Sulekic 810* (14), *1850* (10); *Sundell 6868* (1); *Swallen 1247* (5), *3939* (9), *8385* (4), *8688* (13), *9049* (11), *9201* (11), *9235* (11), *9514* (13), *9519* (13).

Tamayo 3037 (9), *3095* (9), *3566* (13); *Taylor E1296* (9); *Thomas 103070* (3), *142049* (1), *147645* (1), *151215* (1), *155696* (1), *168916* (1); *Tracy 1385* (1), *4538* (3), *7102* (5), *7764* (1), *7766* (1), *8292* (1), *s.n.* (3); *Troncoso 3248* (12); *Tsugaru B-1310* (13).

Vallejo 57 (4); *Van der Sluijs 1435* (13); *Venturi 6761* (13), *10245* (11).

Walker 3222 (1); *Weatherwax 1753* (13); *Williamson s.n.* (1); *Wood 7993* (13), *14470* (13); *Wurdack 39806* (9), *41113* (8a).

Zuloaga 5747 (12), *8658* (10).

NUEVAS SECCIONES EN *BACCHARIS* (ASTERACEAE, ASTEREAE) DE AMÉRICA DEL SUR[1]

Daniel A. Giuliano[2] *y Susana E. Freire*[3]

Resumen

Se describen 15 nuevas secciones del género *Baccharis* L. (Asteraceae, Astereae) de distribución sudamericana, cuatro de ellas pertenecientes al subgénero *Baccharis*: *Baccharis* sect. *Caespitosae* Giuliano, *Baccharis* sect. *Frenguellianae* Giuliano, *Baccharis* sect. *Spicatae* Giuliano y *Baccharis* sect. *Tucumanenses* Giuliano; cinco pertenecientes al subgénero *Molina* (Pers.) Heering: *Baccharis* sect. *Albidae* Giuliano, *Baccharis* sect. *Divaricatae* Giuliano, *Baccharis* sect. *Effusae* Giuliano, *Baccharis* sect. *Lilloanae* Giuliano y *Baccharis* sect. *Megapotamicae* Giuliano; una perteneciente al subgénero *Pteronioides* Heering: *Baccharis* sect. *Australes* Giuliano; una perteneciente al subgénero *Tarchonanthoides* Heering: *Baccharis* sect. *Coridifoliae* Giuliano; y cuatro secciones no asignadas a subgénero alguno: *Baccharis* sect. *Arenariae* Giuliano, *Baccharis* sect. *Rodriguezianae* Giuliano, *Baccharis* sect. *Tenellae* Giuliano y *Baccharis* sect. *Thymifoliae* Giuliano. Se proponen tres nuevas combinaciones: *Baccharis* sect. *Heterothalamus* (Less.) Giuliano, *Baccharis* sect. *Icma* (Phil.) Giuliano y *Baccharis* sect. *Palenia* (Phil.) Giuliano. Se designa un lectotipo para *B. arenaria* Baker.

Abstract

Fifteen new sections of genus *Baccharis* L. (Asteraceae, Astereae) from South America are described, four of them belonging to subgenus *Baccharis*: *Baccharis* sect. *Caespitosae* Giuliano, *Baccharis* sect. *Frenguellianae* Giuliano, *Baccharis* sect. *Spicatae* Giuliano, and *Baccharis* sect. *Tucumanenses* Giuliano; five belonging to subgenus *Molina* (Pers.) Heering: *Baccharis* sect. *Albidae* Giuliano, *Baccharis* sect. *Divaricatae* Giuliano, *Baccharis* sect. *Effusae* Giuliano, *Baccharis* sect. *Lilloanae* Giuliano, and *Baccharis* sect. *Megapotamicae* Giuliano; one belonging to subgenus *Pteronioides* Heering: *Baccharis* sect. *Australes* Giuliano; one belonging to subgenus *Tarchonanthoides* Heering: *Baccharis* sect. *Coridifoliae* Giuliano; and four sections not assigned to any subgenus: *Baccharis* sect. *Arenariae* Giuliano, *Baccharis* sect. *Rodriguezianae* Giuliano, *Baccharis* sect. *Tenellae* Giuliano, and *Baccharis* sect. *Thymifoliae* Giuliano. Three new combinations are proposed: *Baccharis* sect. *Heterothalamus* (Less.) Giuliano, *Baccharis* sect. *Icma* (Phil.) Giuliano, and *Baccharis* sect. *Palenia* (Phil.) Giuliano. A lectotype is designated for *B. arenaria* Baker.

Key words: América del Sur, Asteraceae, Astereae, *Baccharis*.

El género *Baccharis* L. (Asteraceae, Astereae) comprende entre 360 y 400 especies de distribución exclusivamente americana (Bremer, 1994; Nesom & Robinson, 2007). En un trabajo previo (Giuliano, 2001) se estudió la clasificación infragenérica de las especies que crecen en Argentina—aunque su rango de distribución puede alcanzar desde el sur de Estados Unidos hasta el sur de Chile—ubicando a las mismas en 15 secciones; si bien fueron analizados diversos caracteres, los taxones infragenéricos estaban basados principalmente en la arquitectura de las capitulescencias. Luego de un análisis más detallado, incluyendo especialmente microcaracteres tales como el tipo de tricomas en órganos vegetativos y reproductivos, se evidenció que varias de esas secciones en realidad eran agrupamientos de carácter artificial, por lo que la similitud en el tipo de capitulescencia respondería a casos de evolución paralela. En consecuencia, ca. 40 especies—de distribución exclusivamente sudamericana, desde Perú hasta el sur de Chile y Argentina—deben ser removidas de las secciones en las que fueron clasificadas en el estudio previo (Giuliano, 2001); ca. 15 de estas especies pueden ser reubicadas en secciones ya existentes, mientras que otras 25 especies presentan caracteres que las diferencian de las secciones descritas hasta el momento.

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Por lo tanto, el objetivo del presente trabajo es dar a conocer nuevas secciones para incluir a aquellas especies que no se corresponden con los taxones hasta ahora descritos; asimismo, se indican aquellas especies previamente clasificadas (Giuliano, 2001) que son reubicadas en otras secciones (véase el Apéndice 1 para obtener un orden alfabético de los nombres de las especies afectadas y para un resumen de las modificaciones efectuadas).

Tratamiento Taxonómico y Nuevas Secciones en *Baccharis*

Baccharis L., Sp. Pl. 2: 860–861. 1753. TIPO CONSERVADO: *Baccharis halimifolia* L., Sp. Pl. 2: 860–861. 1753, designado por Hitchcock y Greene (1929: 181); propuesto para su conservación por Hellwig (1989: 513–515) (véase también Brummitt [1993: 693]).

Baccharis subg. **Baccharis**.

I. Baccharis secc. **Caespitosae** Giuliano, sect. nov. TIPO: *Baccharis caespitosa* (Ruiz & Pav.) Pers. [≡ *Molina caespitosa* Ruiz & Pav.].

Sectio ad *Baccharidem* L. subg. *Baccharidem* pertinens, sectioni *Cuneifoliis* DC. capitulis plerumque solitariis ad apicem ramorum involucro falso foliorum parvorum circumcinctis similis, sed ab ea trichomatum uniseriatorum caespitum pilosorum cellulis apicalibus flagelliformibus ac parietibus tenuibus differt.

Arbustos erectos o rastreros; indumento constituido por diminutos pelos glandulares biseriados y pelos no glandulares uniseriados con célula apical flageliforme, agrupados en manojos (nidos pilosos, Ariza Espinar, 1973). Hojas sésiles o pseudopecioladas, enteras o paucidentadas, en apariencia uninervadas (con sólo la nervadura media notoria). Capítulos sésiles o pedunculados, solitarios en el extremo de las ramas o reunidos formando una sinflorescencia racemiforme o paniculiforme, o bien dispuestos en la axila de las hojas superiores formando un glomérulo folioso; involucros acampanados; receptáculos planos a cónicos, desprovistos de páleas; proporción de flores carpeladas:estaminadas ca. 1:1. Corola de las flores carpeladas con ápice 5-denticulado; aquenios teretes, (6-)7- a 12-costados, glabros, sin papilas, no visibles debajo del involucro a la madurez; cerdas del papus de las flores carpeladas dispuestas en 2 series, acrescentes, caducas. Corola de las flores estaminadas con limbo gradualmente diferenciado del tubo; ápice del estilo obtrulado, con ramas breves y mayormente adheridas entre sí; cerdas del papus de las flores estaminadas con ápice levemente ensanchado.

Distribución. Comprende tres especies, propias de la región andina de Perú, Bolivia, Chile y Argentina (Hellwig, 1990; Giuliano, 2000, 2008; Müller, 2006).

ESPECIES INCLUIDAS

1. Baccharis caespitosa (Ruiz & Pav.) Pers., Syn. Pl. 2: 425. 1807. Basiónimo: *Molina caespitosa* Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 203. 1798. TIPO: Perú. Junín: "Punas de Bombom", s.d., *Ruiz & Pavón s.n.* (lectotipo, designado por Müller [2006: 83], MA foto en LP!).

2. Baccharis santelicis Phil., Anales Mus. Nac., Santiago de Chile 8: 39. 1891.

3. Baccharis tola Phil., Fl. Atacama: 30. 1860.

Estas especies fueron anteriormente ubicadas en *Baccharis* secc. *Cuneifoliae* DC. (Giuliano, 2001), por poseer capítulos sésiles solitarios en el ápice de las ramas, cada uno rodeado por un falso involucro de pequeñas hojas, a veces reunidos en sinflorescencias racemiformes; no obstante, este taxón debe reservarse para incluir a su especie tipo, *B. cuneifolia* (Lam.) DC. [= *B. patagonica* Hook. & Arn.], y especies afines (e.g., *B. elaeoides* J. Rémy, *B. macraei* Hook. & Arn., *B. pilcensis* F. H. Hellw., *B. rhomboidalis* J. Rémy). La nueva sección *Caespitosae* se diferencia por poseer los pelos uniseriados de los nidos pilosos con célula apical flageliforme y con paredes delgadas (vs. célula apical triangular y con paredes gruesas en sección *Cuneifoliae*). La nueva sección *Caespitosae* concuerda con el grupo informal de *B. caespitosa* propuesto por Müller (2006).

Por otra parte, *Baccharis triangularis* Hauman, incluida en la sección *Cuneifoliae* (Giuliano, 2001) por la presencia de capítulos terminales sésiles solitarios o poco agrupados, cada uno rodeado por un falso involucro de pequeñas hojas, debe ser retransferida a la sección *Caulopterae* DC. del subgénero *Molina* (Pers.) Heering por presentar tallos alados (vs. tallos no alados en sección *Cuneifoliae*), estilos de las flores estaminadas con ápice no obtrulado (vs. estilos con ápice obtrulado) y cerdas del papus de las flores estaminadas con ápice no ensanchado (vs. cerdas con ápice ensanchado).

II. Baccharis secc. **Frenguellianae** Giuliano, sect. nov. TIPO: *Baccharis frenguellii* Cabrera.

Sectio ad *Baccharidem* L. subg. *Baccharidem* pertinens, a ceteris sectionibus hujus subgeneris capitulis brevissime pedunculatis solitariis vel paucis racemum foliosum laxum formantibus, corolla florum carpellatorum apice 5-denticulata et pappo florum staminatorum apice leviter dilatato conjunctim praesentibus differt.

Arbustos erectos; indumento constituido por diminutos pelos glandulares biseriados y pelos no glandulares uniseriados con célula apical breve y de ápice redondeado, agrupados en nidos. Hojas sésiles, las inferiores paucidentadas y trinervadas, las superiores enteras y en apariencia uninervadas. Capítulos brevísimamente pedunculados, solitarios o agrupados en corto número formando un racimo folioso laxo en el ápice de las ramas; involucros acampanados; receptáculos planos, desprovistos de páleas; proporción de flores carpeladas:estaminadas ca. 1:1. Corola de las flores carpeladas con ápice 5-denticulado; aquenios teretes, 10- a 12-costados, glabros, sin papilas, no visibles debajo del involucro a la madurez; cerdas del papus de las flores carpeladas dispuestas en 2 series, acrescentes, caducas. Corola de las flores estaminadas con limbo gradualmente diferenciado del tubo; ápice del estilo obtrulado, con ramas breves y mayormente adheridas entre sí; cerdas del papus de las flores estaminadas con ápice levemente ensanchado.

Distribución. La nueva sección comprende una sola especie, propia de Paraguay y el nordeste de Argentina (Cabrera, 1974; Soria & Zardini, 1995; Giuliano, 2000, 2008).

ESPECIE INCLUIDA

1. **Baccharis frenguellii** Cabrera, Darwiniana 16: 409. 1970. TIPO: Argentina. Entre Ríos: Paraná, 23 mayo 1940, *Cabrera 6485* (holotipo, LP!).

Esta especie fue anteriormente clasificada en la sección *Discolores* DC. (Giuliano, 2001); sin embargo, este taxón debe reservarse para incluir a su especie lectotipo, *Baccharis phylicoides* Kunth. *Baccharis frenguellii* se diferencia de ella por poseer los pelos uniseriados de los nidos pilosos con célula apical breve (vs. célula apical filiforme en *B. phylicoides*) y los capítulos dispuestos en racimos laxos (vs. espigas o racimos densos). *Baccharis caprariifolia* DC., *B. dracunculifolia* DC. y *B. tandilensis* Speg., previamente incluidas en la sección *Discolores* (Giuliano, 2001), como *B. elaeagnoides* Steud. ex Baker y *B. semiserrata* DC. (incluidas en la sección *Nitidae* Cuatrec. [Giuliano, 2001, 2005]), corresponden mejor a la rehabilitada sección *Racemosae* Ariza, caracterizada por los pelos uniseriados de los nidos pilosos con célula apical ramificada.

III. Baccharis secc. **Spicatae** Giuliano, sect. nov. TIPO: *Baccharis spicata* (Lam.) Baill. [≡ *Eupatorium spicatum* Lam.].

Sectio ad *Baccharidem* L. subg. *Baccharidem* pertinens, sectioni *Baccharidi* capitulis basalibus synflorescentiarum in glomerulos pedunculatos dispositis similis, sed ab ea capitulis apicalibus in glomerulos sessiles spicatos dispositis et pappo florum carpellatorum non accrescenti differt.

Subarbustos erectos; indumento constituido por diminutos pelos glandulares biseriados y pelos no glandulares uniseriados con célula apical terminada en un flagelo muy largo, agrupados en nidos. Hojas inferiores opuestas, las superiores alternas o subopuestas, pseudopecioladas, paucidentadas, uni- o trinervadas. Capítulos sésiles, en glomérulos intercalados con capítulos solitarios, formando una espiga foliosa en el extremo de las ramas y de ramitas laterales, si bien en estas últimas pueden presentarse glomérulos solitarios; involucros acampanados; receptáculos cónicos, desprovistos de páleas; proporción de flores carpeladas:estaminadas ca. 2:1. Corola de las flores carpeladas con ápice irregularmente 5-dentado; aquenios teretes, 8- a 10-costados, glabros, sin papilas, no visibles debajo del involucro a la madurez; cerdas del papus de las flores carpeladas dispuestas en 2 series, no acrescentes, caducas. Corola de las flores estaminadas con limbo gradualmente diferenciado del tubo; ápice del estilo obtrulado, con ramas breves y mayormente adheridas entre sí; cerdas del papus de las flores estaminadas con ápice no ensanchado.

Distribución. Baccharis secc. *Spicatae* comprende una sola especie, propia del sur de Brasil, Paraguay, Uruguay y nordeste y centro de Argentina (Barroso, 1976; Soria & Zardini, 1995; Giuliano, 2000, 2008).

ESPECIE INCLUIDA

1. **Baccharis spicata** (Lam.) Baill., Bull. Mens. Soc. Linn. Paris 34: 268. 1880. Basiónimo: *Eupatorium spicatum* Lam., Encycl. (Lamarck) 2: 409. 1786. TIPO: Uruguay. Montevideo, s.d., *Commerson 111* (holotipo, P no visto).

Esta especie fue anteriormente ubicada en la sección *Baccharis* (Giuliano, 2001), por poseer los capítulos basales de la sinflorescencia dispuestos en glomérulos pedunculados; no obstante, este taxón

debe reservarse para incluir a su especie tipo, *B. halimifolia* L., y especies afines (e.g., *B. emoryi* A. Gray, *B. neglecta* Britton, *B. salicina* Torr. & A. Gray, *B. sergiloides* A. Gray). La nueva sección *Spicatae* se diferencia por los capítulos apicales de la sinflorescencia dispuestos en glomérulos sésiles espigados (vs. capítulos solitarios y/o dispuestos en glomérulos pedunculados, no espigados, en sección *Baccharis*) y el papus de las flores carpeladas no acrescente (vs. notablemente acrescente).

IV. Baccharis secc. **Tucumanenses** Giuliano, sect. nov. TIPO: *Baccharis tucumanensis* Hook. & Arn.

Sectio ad *Baccharidem* L. subg. *Baccharidem* pertinens, a ceteris sectionibus hujus subgeneris foliis uni- vel pinnatinerviis, capitulis in glomerulos solitarios vel spicatos dispositis et pappo florum carpellatorum non accrescenti conjunctim praesentibus differt.

Arbustos erectos; indumento constituido por diminutos pelos glandulares biseriados y pelos no glandulares uniseriados con célula apical breve o largamente flagelada, agrupados en nidos. Hojas pseudopecioladas o pecioladas, enteras o dentadas, uni- o penninervadas. Capítulos sésiles, solitarios en los ápices de las ramas o dispuestos en glomérulos foliosos simples terminales, o bien en glomérulos agrupados formando una espiga foliosa en el extremo de las ramas y de ramitas laterales, si bien en estas últimas pueden presentarse glomérulos solitarios; involucros acampanados; receptáculos convexos o cónicos, desprovistos de páleas; proporción de flores carpeladas:estaminadas ca. 1:1. Corola de las flores carpeladas con ápice irregularmente 5-dentado; aquenios teretes, 5- a 12-costados, glabros, sin papilas, no visibles debajo del involucro a la madurez; cerdas del papus de las flores carpeladas dispuestas en 2 series, acrescentes, caducas. Corola de las flores estaminadas con limbo gradualmente diferenciado del tubo; ápice del estilo obtrulado, con ramas breves y mayormente adheridas entre sí; cerdas del papus de las flores estaminadas con ápice ensanchado.

Distribución. *Baccharis* secc. *Tucumanenses* comprende cuatro especies del sur de Bolivia y el noroeste de Argentina (Giuliano, 2000, 2008; Müller, 2006).

ESPECIES INCLUIDAS

1. **Baccharis famatinensis** Ariza, Lorentzia 2: 5. 1973.

2. **Baccharis kurtziana** Ariza, Kurtziana 6: 69. 1971.

3. **Baccharis rupestris** Heering, Jahrb. Hamburg. Wiss. Anst. 31(3): 132. 1915.

4. **Baccharis tucumanensis** Hook. & Arn., J. Bot. (Hooker) 3: 34. 1840. TIPO: Argentina. Tucumán: San Javier, s.d., *Tweedie 1199* (lectotipo, designado por Müller [2006: 54], K foto en LP!).

Baccharis famatinensis y *B. tucumanensis* fueron anteriormente incluidas en la sección *Baccharis* (Giuliano, 2001) por presentar capítulos en glomérulos pedunculados, mientras que *B. kurtziana* y *B. rupestris* fueron ubicadas en la sección *Cuneifoliae* (Giuliano, 2001) debido a sus capítulos solitarios o en pequeños grupos; sin embargo, estas especies son claramente afines y deben agruparse bajo un mismo taxón, como propone Müller (2006) al reunirlas en el grupo informal de *B. tucumanensis*.

Baccharis subg. **Molina** (Pers.) Heering en Reiche, Anales Univ. Chile 111: 155. 1902. TIPO: *Baccharis latifolia* (Ruiz & Pav.) Pers. [≡ *Molina latifolia* Ruiz & Pav.] (lectotipo, designado por Cuatrecasas [1967: 87]).

I. Baccharis secc. **Albidae** Giuliano, sect. nov. TIPO: *Baccharis albida* Hook. & Arn.

Sectio ad *Baccharidem* subgen. *Molinam* (Pers.) Heering pertinens, sectioni *Molinae* (Pers.) Cuatrec. foliis trinerviis et capitulis in corymbos compositos terminales dispositis similis, sed ab ea habitu herbaceo et indumento denso trichomatibus uniseriatis 2-cellularibus in caespites non aggregatis differt.

Hierbas perennes; indumento constituido por pelos no glandulares uniseriados 2-celulares, con célula basal elongada y célula apical terminada en un flagelo muy largo, no agrupados en nidos; estos pelos se presentan densamente dispuestos formando una pubescencia lanuginosa. Hojas brevísimamente pecioladas, aserradas, trinervadas. Capítulos pedunculados, dispuestos en corimbos compuestos terminales; involucros acampanados; receptáculos cónicos, desprovistos de páleas; proporción de flores carpeladas: estaminadas ca. 6:1. Corola de las flores carpeladas con ápice truncado; aquenios teretes, 5-costados, con papilas elongadas densamente dispuestas, no visibles debajo del involucro a la madurez; cerdas del papus de las flores carpeladas dispuestas en una sola serie, no acrescentes, persistentes. Corola de las flores estaminadas con limbo bien diferenciado del tubo; estilo con ramas lanceoladas y separadas; cerdas del

papus de las flores estaminadas con ápice levemente ensanchado.

Distribución. *Baccharis* secc. *Albidae* comprende una sola especie, endémica del nordeste de Argentina (Cabrera, 1974; Giuliano, 2000, 2008).

ESPECIE INCLUIDA

1. Baccharis albida Hook. & Arn. in Hook., J. Bot. (Hooker) 3: 41. 1840. TIPO: Argentina. Santa Fe, s.d., *Tweedie s.n.* (holotipo, K no visto, K000221997 imagen digitalizada! [en sitio web de Royal Botanic Gardens, Kew, http://apps.kew.org/herbcat/navigator.do]).

Esta especie fue previamente incluida en la sección *Molina* (Pers.) Cuatrec. (Giuliano, 2001), por presentar hojas trinervadas y capítulos dispuestos en corimbos compuestos terminales, pero se diferencia de este taxón por el hábito herbáceo (vs. hábito arbustivo en sección *Molina*) y el indumento conspicuo y denso constituido por pelos no glandulares uniseriados 2-celulares no agrupados en nidos (vs. indumento inconspicuo constituido por diminutos pelos glandulares biseriados y pelos no glandulares uniseriados agrupados en nidos). *Baccharis glutinosa* Pers. y *B. stenophylla* Ariza, asimismo incluidas anteriormente en la sección *Molina* (Giuliano, 2001, la primera sub *B. pingraea* DC.), pertenecen mejor a la sección *Baccharidastrum* (Cabrera) G. L. Nesom, debido al hábito herbáceo o subarbustivo (vs. hábito arbustivo en sección *Molina*) y a los aquenios provistos de pelos unicelulares papiliformes elongados (vs. aquenios con pelos gemelos o glabros).

Por otra parte, *Baccharis oxyodonta* DC. y *B. punctulata* DC., anteriormente ubicadas en la sección *Trinervatae* DC. (Giuliano, 2001) por presentar capítulos dispuestos en una sinflorescencia paniculiforme, deben ser incluidas en la sección *Molina* dada la presencia de hábito erecto (vs. hábito escandente en sección *Trinervatae*) y la ausencia de páleas en los receptáculos de los capítulos carpelados (vs. páleas presentes).

Baccharis polygama Ariza, clasificada en la heterogénea sección *Aristidentes* G. L. Nesom (Giuliano, 2001; véanse más adelante los comentarios para las nuevas secciones *Lilloanae* y *Australes*), pertenece al subgénero *Molina* por presentar aquenios 5-costados con papus uniseriado ligeramente acrescente; tentativamente se propone aquí ubicarla en la sección *Molina*, en virtud de presentar hábito arbustivo erecto y capítulos dispuestos en corimbos compuestos terminales, aunque presenta algunas diferencias tales como la presencia de hojas con la vena media notoria y venas secundarias inconspicuas (vs. hojas tri- o penninervadas en sección *Molina*), capítulos estaminados heterógamos (vs. capítulos estaminados homógamos; excepcionalmente se pueden presentar capítulos heterógamos en *B. salicifolia* (Ruiz & Pav.) Pers.), capitulescencias congestas (vs. capitulescencias laxas) y cerdas del papus de las flores estaminadas con ápice apenas denticulado, no ensanchado (vs. cerdas con ápice ensanchado).

II. Baccharis secc. **Divaricatae** Giuliano, sect. nov. TIPO: *Baccharis divaricata* Hauman.

Sectio ad *Baccharidem* subgen. *Molinam* (Pers.) Heering pertinens, pluribus speciebus sectionis *Caulopterarum* DC. foliis minutis bracteiformibus, acheniis 8- ad 10-costatis et pappo florum carpellatorum biseriato accrescenti similis, sed ab eis ramis divaricatis, capitulis ad apicem ramulorum brevium in paniculam amplam dispositis, involucris capitulorum carpellatorum campanulatis et pappo florum staminatorum regulariter denticulato differt.

Subarbustos erectos con ramas divaricadas; indumento constituido por diminutos pelos glandulares biseriados y pelos no glandulares uniseriados con célula apical flageliforme, agrupados en nidos (a veces los nidos presentan sólo pelos no glandulares). Hojas de las ramas jóvenes pequeñas, sésiles, enteras, en apariencia uninervadas; hojas de las ramas adultas reducidas a brácteas inconspicuas. Capítulos dispuestos en el extremo de ramitas breves (los apicales generalmente sésiles en el eje de las ramitas), reunidos en una panícula muy amplia; involucros acampanados; receptáculos planos o levemente convexos, desprovistos de páleas; proporción de flores carpeladas:estaminadas ca. 1:1. Corola de las flores carpeladas con ápice irregularmente 5-dentado; aquenios teretes, 8- a 10-costados, glabros, con papilas, no visibles debajo del involucro a la madurez; cerdas del papus de las flores carpeladas dispuestas en 2 series, acrescentes, persistentes. Corola de las flores estaminadas con limbo abruptamente diferenciado del tubo; estilo con ramas breves pero separadas; cerdas del papus de las flores estaminadas con ápice regularmente denticulado, no ensanchado.

Distribución. *Baccharis* secc. *Divaricatae* comprende una sola especie, endémica de las dunas del litoral atlántico de Argentina (Cabrera, 1971; Giuliano, 2000, 2008).

ESPECIE INCLUIDA

1. Baccharis divaricata Hauman, Anales Mus. Nac. Hist. Nat. Buenos Aires 24: 429, fig. 19. 1913.

TIPO: Argentina. Río Negro: en las dunas, cerca de la embocadura, feb. 1912, *Hauman s.n.* (holotipo, BA no visto, imagen digitalizada!).

Esta especie, previamente incluida en la sección *Baccharis* (Giuliano, 2001), presenta algunos caracteres en común con el subgénero *Baccharis*, e.g., la proporción de flores carpeladas:estaminadas ca. 1:1, la corola de las flores carpeladas con ápice irregularmente 5-dentado, los aquenios 8- a 10-costados glabros y las cerdas del papus de las flores carpeladas biseriadas y acrescentes; no obstante, se diferencia por caracteres como la corola de las flores estaminadas con el limbo abruptamente diferenciado del tubo (vs. corola con el limbo gradualmente diferenciado del tubo en subgénero *Baccharis*), el estilo de las flores estaminadas con el ápice no obtrulado con ramas breves pero separadas (vs. estilo con ápice obtrulado con ramas breves y adheridas) y las cerdas del papus de las flores estaminadas con ápice regularmente denticulado, no ensanchado en el ápice (vs. cerdas con ápice ensanchado). Por otra parte, *B. divaricata* presenta caracteres en común con varias especies de la sección *Caulopterae* del subgénero *Molina*, e.g., la condición subáfila, los aquenios 8- a 10-costados y las cerdas del papus de las flores carpeladas biseriadas y acrescentes; de hecho, Müller (2006) ubicó a esta especie en el grupo informal de *B. aphylla* (Vellozo) DC.—aquí considerado como parte de la sección *Caulopterae*—pero la presencia de diferencias tales como las ramas divaricadas (vs. ramas ascendentes no divaricadas en sección *Caulopterae*), los capítulos dispuestos en el extremo de ramitas breves (los apicales generalmente sésiles), reunidos en una panícula muy amplia (vs. capítulos consistentemente sésiles, dispuestos en espigas o glomérulos), los involucros de los capítulos carpelados acampanados (vs. involucros de los capítulos carpelados cilíndricos) y las cerdas del papus de las flores estaminadas regularmente denticuladas (vs. cerdas lisas) justifican su inclusión en una sección propia.

III. Baccharis secc. **Effusae** Giuliano, sect. nov. TIPO: *Baccharis effusa* Griseb.

Sectio ad *Baccharidem* subg. *Molinam* (Pers.) Heering pertinens, a ceteris sectionibus hujus subgeneris foliis linearibus ut videtur uninerviis, capitulis in synflorescentias paniculiformes dispositis et pappo florum carpellatorum accrescenti differt.

Arbustos erectos; indumento constituido por diminutos pelos glandulares biseriados y pelos no glandulares uniseriados con célula apical flageliforme, agrupados en nidos (a veces los nidos presentan sólo pelos glandulares o pelos no glandulares). Hojas sésiles, enteras, en apariencia uninervadas. Capítulos pedunculados, dispuestos en el extremo de ramitas muy breves formando un racimo folioso; el conjunto de las ramas compone una amplia sinflorescencia paniculiforme; involucros acampanados; receptáculos planos o levemente convexos, desprovistos de páleas; proporción de flores carpeladas:estaminadas ca. 2:1. Corola de las flores carpeladas con ápice truncado y con una corona de pelos biseriados; aquenios teretes, 5- a 8-costados, subglabros, con pocos pelos glandulares biseriados, sin papilas, no visibles debajo del involucro a la madurez; cerdas del papus de las flores carpeladas dispuestas en una sola serie, acrescentes, persistentes. Corola de las flores estaminadas con limbo bien diferenciado del tubo; estilo con ramas lanceoladas y separadas; cerdas del papus de las flores estaminadas con ápice levemente ensanchado.

Distribución. *Baccharis* secc. *Effusae* comprende una sola especie, propia del centro y sur de Bolivia y el noroeste de Argentina (Giuliano, 2000, 2008; Müller, 2006).

ESPECIE INCLUIDA

1. Baccharis effusa Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 177. 1874. TIPO: Argentina. Tucumán: pr. Juntas, 28 Mar. 1872, *Lorentz 140* (holotipo, GOET no visto; isotipo, B†, B foto serie F.M. n° 14969 en LP!).

Esta especie se diferencia de las demás secciones del subgénero *Molina* por las hojas lineares en apariencia uninervadas, los capítulos dispuestos en sinflorescencias paniculiformes y las cerdas del papus de las flores carpeladas acrescentes. Anteriormente fue ubicada en la sección *Paniculatae* Heering (Giuliano, 2001), por la presencia de hojas lineares en apariencia uninervadas y la disposición de los capítulos en sinflorescencias paniculiformes; no obstante, este taxón debe reservarse para incluir a su especie tipo, *Baccharis paniculata* DC., correspondiente al subgénero *Pteronioides* Heering, de la cual *B. effusa* se diferencia por presentar proporción de flores carpeladas:estaminadas ca. 2:1 (vs. ca. 1:1 en sección *Paniculatae*), aquenios con escasos pelos glandulares biseriados, no visibles debajo del involucro a la madurez (vs. aquenios con pelos no glandulares uniseriados y glandulares biseriados, visibles debajo del involucro) y cerdas del papus de las flores carpeladas uniseriadas (vs. biseriadas). La similitud en el tipo de sinflorescencia encontrado en las especies de la sección *Coridifoliae* del subgénero

Tarchonanthoides Heering (véase más adelante), también clasificadas en la sección *Paniculatae* (Giuliano, 2001), es asimismo superficial. *Baccharis effusa* se diferencia de estas especies por poseer pelos glandulares y no glandulares agrupados en nidos (vs. pelos no glandulares filiformes y flageliformes no agrupados en nidos en sección *Coridifoliae*), proporción de flores carpeladas:estaminadas ca. 2:1 (vs. ca. 1:1), flores carpeladas con corolas de ápice truncado (vs. regularmente 5-dentado) y cerdas del papus de las flores carpeladas uniseriadas (vs. biseriadas).

IV. Baccharis secc. **Lilloanae** Giuliano, sect. nov. TIPO: *Baccharis lilloi* Heering.

Sectio ad *Baccharidem* subg. *Molinam* (Pers.) Heering pertinens, sectioni *Scandentibus* Cuatrec. indumento ex trichomatibus eglandulosis conicis, eglandulosis uniseriatis flagelliformibus et glandulosis biseriatis in caespites non aggregatis constanti similis, sed ab ea habitu erecto et foliis reticulato-veniis differt.

Arbustos erectos; indumento constituido por pelos no glandulares uniseriados cónicos con pedestal (la porción basal a veces pluriseriada), pelos no glandulares uniseriados con célula apical flageliforme y pelos glandulares biseriados, no agrupados en nidos; estos pelos se presentan densamente dispuestos formando una pubescencia tomentosa. Hojas sésiles o brevemente pecioladas, enteras o dentadas, retinervadas. Capítulos pedunculados, dispuestos en corimbos simples o compuestos terminales o en el ápice de ramitas laterales; involucros acampanados; receptáculos planos o convexos, desprovistos de páleas; proporción de flores carpeladas:estaminadas 1:1 a 3:1. Corola de las flores carpeladas con ápice truncado y con una corona de pelos; aquenios teretes, 5- a 8-costados, con pelos gemelos y pelos glandulares biseriados, con papilas, no visibles debajo del involucro a la madurez; cerdas del papus de las flores carpeladas dispuestas en una sola serie, no acrescentes, persistentes. Corola de las flores estaminadas con limbo bien diferenciado del tubo; estilo con ramas lanceoladas y separadas; cerdas del papus de las flores estaminadas con ápice levemente o no ensanchado.

Distribución. *Baccharis* secc. *Lilloanae* comprende dos especies, propias del sur de Bolivia y el noroeste de Argentina (Giuliano, 2000, 2008; Müller, 2006).

ESPECIES INCLUIDAS

1. Baccharis lilloi Heering, Jahrb. Hamburg. Wiss. Anst. 31(3): 78. 1915. TIPO: Argentina. Tucumán: Dpto. Tafí, El Rincón, 2250 m, 4 Feb. 1908, *Lillo 7533* (lectotipo, designado por Müller [2006: 188], HBG no visto).

2. Baccharis multiflosculosa Heering, Jahrb. Hamburg. Wiss. Anst. 31(3): 79. 1915.

Estas especies se asemejan a las de la sección *Scandentes* Cuatrec. por el indumento constituido por pelos uniseriados cónicos con pedestal, pelos uniseriados flageliformes y pelos glandulares biseriados no agrupados en nidos y por los aquenios papilosos, pero se diferencian por el hábito erecto (vs. hábito escandente en sección *Scandentes*), las hojas retinervadas (vs. hojas trinervadas) y los aquenios con pelos glandulares biseriados (vs. aquenios sin pelos glandulares biseriados). Anteriormente fueron ubicadas en la sección *Aristidentes* (Giuliano, 2001); no obstante, este taxón debe reservarse para incluir a su especie tipo, *Baccharis multiflora* Kunth, y especies afines (*B. plummerae* A. Gray, *B. serrifolia* DC., *B. sordescens* DC.), correspondiente al subgénero *Pteronioides* (véase más adelante el comentario para la nueva sección *Australes* de ese subgénero). *Baccharis lilloi* y *B. multiflosculosa* pertenecen al subgénero *Molina* en virtud de la proporción de flores carpeladas:estaminadas 1:1 a 3:1 (vs. ca. 1:1 en subgénero *Pteronioides*), los aquenios con pelos gemelos y papilas, no visibles debajo del involucro a la madurez (vs. aquenios con pelos no glandulares uniseriados y glandulares biseriados, generalmente sin papilas, visibles debajo del involucro), y las cerdas del papus de las flores carpeladas uniseriadas no acrescentes (vs. biseriadas acrescentes). La sección *Lilloanae* se corresponde con el grupo informal de *B. lilloi* propuesto por Müller (2006).

Baccharis multiflosculosa fue previamente considerada sinónimo de *B. pulchella* Sch. Bip. ex Griseb. (Giuliano, 2000, 2001, 2008), aunque la similitud entre ambas es superficial, como fue evidenciado por Müller (2006); esta última especie, asimismo incluida en la sección *Aristidentes* (Giuliano, 2001), pertenece a la sección *Tubulatae* Cuatrec. del subgénero *Pteronioides*.

Cabe asimismo aclarar aquí que *Baccharis anomala* DC., previamente clasificada en la sección *Trinervatae* del subgénero *Molina* (Giuliano, 2001) en virtud del hábito escandente y las hojas trinervadas, debe incluirse en la rehabilitada sección *Scandentes* del mismo subgénero debido al indumento constituido por pelos uniseriados cónicos con pedestal y pelos uniseriados flageliformes no agrupados en nidos (vs. pelos agrupados en nidos, a veces acompañados o reemplazados por pelos filiformes o ramificados aislados en sección *Trinervatae*) y a la

ausencia de páleas en los receptáculos de los capítulos carpelados (vs. páleas presentes).

V. Baccharis secc. **Megapotamicae** Giuliano, sect. nov. TIPO: *Baccharis megapotamica* Spreng.

Sectio ad *Baccharidem* subg. *Molinam* (Pers.) Heering pertinens, sectioni *Caulopteris* DC. capitulis sessilibus, ratione florum carpellatorum cum staminatis ca. 2:1, acheniis 10-costatis et pappo florum staminatorum apice non dilatato similis, sed ab ea indumento ex trichomatibus eglandulosis uniseriatis apice incurvato cellulaque apicali pyriformi in caespites non aggregatis constanti et capitulis in axillas foliorum apicalium conjunctim spicam foliosam formantibus differt.

Arbustos erectos; indumento constituido por pelos no glandulares uniseriados con ápice incurvado y célula apical piriforme no agrupados en nidos, acompañados por otros pelos similares pero mucho más pequeños. Hojas sésiles o pseudopecioladas, enteras y revolutas, en apariencia uninervadas, ligeramente discoloras. Capítulos sésiles, solitarios en la axila de las hojas superiores, formando en conjunto una espiga foliosa; involucros acampanados; receptáculos planos, desprovistos de páleas; proporción de flores carpeladas:estaminadas ca. 2:1. Corola de las flores carpeladas con ápice truncado o 5-denticulado; aquenios teretes, 10-costados, glabros, con papilas, no visibles debajo del involucro a la madurez; cerdas del papus de las flores carpeladas dispuestas en 1 serie, no acrescentes, persistentes. Corola de las flores estaminadas con limbo gradualmente diferenciado del tubo; estilo con ramas lanceoladas y separadas; cerdas del papus de las flores estaminadas con ápice no ensanchado.

Distribución. *Baccharis* secc. *Megapotamicae* comprende una sola especie, propia del sur de Brasil, Paraguay, Uruguay y nordeste de Argentina (Barroso, 1976; Soria & Zardini, 1995; Giuliano, 2000, 2008).

ESPECIE INCLUIDA

1. Baccharis megapotamica Spreng., Syst. Veg. (ed. 16) [Sprengel] 3: 461. 1826. TIPO: Brasil. Río Grande do Sul, s.d., *Sello d1967* [ex Herb. Mus. Imp. Brasiliensis n° 818] (holotipo, P no visto; isotipo, K foto en LP!).

Esta especie, previamente incluida en la sección *Discolores* (Giuliano, 2001), corresponde al subgénero *Molina*, siendo afín a la sección *Caulopterae* por la presencia de capítulos sésiles, proporción de flores carpeladas:estaminadas ca. 2:1, aquenios 10-costados y cerdas del papus de las flores estaminadas con ápice no ensanchado; sin embargo, se diferencia de la misma por la presencia de pelos no glandulares uniseriados de ápice incurvado y célula apical piriforme no agrupados en nidos (vs. pelos glandulares biseriados y no glandulares uniseriados con célula apical usualmente triangular o flageliforme agrupados en nidos en sección *Caulopterae*) y los capítulos dispuestos en la axila de las hojas superiores formando en conjunto una espiga foliosa (vs. capítulos solitarios y/o dispuestos en glomérulos acompañados por brácteas inconspicuas).

Baccharis subg. **Pteronioides** Heering, Jahrb. Hamburg. Wiss. Anst. 21(3): 15. 1904. TIPO: *Baccharis pteronioides* DC.

Observaciones. Hellwig (1993: 211) otorgó a esta especie el carácter de lectotipo; no obstante, según el *International Code of Botanical Nomenclature* (McNeill et al., 2006: Art. 22.6), la misma debe considerarse como holotipo.

I. Baccharis secc. **Australes** Giuliano, sect. nov. TIPO: *Baccharis racemosa* (Ruiz & Pav.) DC. [≡ *Molina racemosa* Ruiz & Pav.].

Sectio ad *Baccharidem* subg. *Pteronioides* Heering pertinens, sectioni *Aristidentibus* G. L. Nesom foliis reticulato-veniis, synflorescentiis paniculiformibus et involucris capitulorum staminatorum hemisphaericis vel subcampanulatis similis, sed ab ea habitu fulto differt.

Arbustos apoyantes; indumento constituido por pelos uniseriados con pedestal largos rectos y con célula apical alargada o flageliforme, y pelos breves incurvados con célula apical alargada de paredes delgadas y ápice redondeado, no agrupados en nidos. Hojas sésiles o brevemente pecioladas, enteras o dentadas, retinervadas. Capítulos pedunculados, dispuestos en corimbos que usualmente se agrupan en racimos axilares y terminales, formando en conjunto una amplia sinflorescencia paniculiforme; involucros de los capítulos carpelados acampanados, los de los estaminados hemisféricos; receptáculos planos o levemente convexos, desprovistos de páleas; proporción de flores carpeladas:estaminadas ca. 1:1. Corola de las flores carpeladas con ápice truncado y con una corona de pelos; aquenios teretes o comprimidos, 5- a 7-costados, con pelos no glandulares uniseriados con célula apical aguda, usualmente acompañados por pelos glandulares biseriados, sin papilas, visibles debajo del involucro a la madurez; cerdas del papus de las flores carpeladas dispuestas en 1 ó 2 series, acrescentes, persistentes.

Corola de las flores estaminadas con limbo bien diferenciado del tubo; estilo con ramas lanceoladas y separadas; cerdas del papus de las flores estaminadas con ápice ensanchado.

Distribución. *Baccharis* secc. *Australes* comprende una sola especie, propia de la región subantártica de Chile y Argentina (Cabrera, 1971; Giuliano, 2000, 2008).

ESPECIE INCLUIDA

1. Baccharis racemosa (Ruiz & Pav.) DC., Prodr. 5: 401. 1836. Basiónimo: *Molina racemosa* Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 1: 209. 1798. TIPO: Chile. Concepción, s.d., *Ruiz y Pavón s.n.* (lectotipo, designado por Cabrera [1960: 202], MA foto en LP!).

Baccharis racemosa fue anteriormente ubicada en la sección *Aristidentes* (Giuliano, 2001), a la que se asemeja por las hojas retinervadas, las sinflorescencias paniculiformes y los capítulos estaminados con involucro hemisférico o subacampanado; sin embargo, se diferencia por el hábito apoyante (vs. erecto en sección *Aristidentes*). Asimismo, la distribución geográfica de ambos taxones es notablemente disyunta. La única especie de la sección *Australes* es exclusiva de la región subantártica de Chile y Argentina, mientras que las especies de la sección *Aristidentes* son propias de Norte y Centroamérica; la inclusión previa de otra especie sudamericana, *B. hirta* DC., en la sección *Aristidentes* (Giuliano & Nesom, 2003) debe ser reevaluada.

Por otra parte, resultaría conveniente realizar estudios para establecer si *Baccharis sessilifolia* DC. es parte de la variabilidad morfológica exhibida por *B. racemosa* o bien si debe ser considerada como taxón independiente.

Baccharis subg. **Tarchonanthoides** Heering, Jahrb. Hamburg. Wiss. Anst. 21(3): 26. 1904. TIPO: *Baccharis tarchonanthoides* DC. [véase comentario más adelante].

I. Baccharis secc. **Coridifoliae** Giuliano, sect. nov. TIPO: *Baccharis coridifolia* DC.

Sectio ad *Baccharidem* subg. *Tarchonanthoides* Heering pertinens, a sectione *Tarchonanthoidibus* (Heering) Cuatrec. foliis sessilibus ut videtur uninerviis et pappo florum carpellatorum biseriato accrescenti differt.

Subarbustos erectos; indumento constituido por pelos uniseriados con célula apical filiforme, usualmente dispuestos densamente formando una pubescencia lanuginosa, a veces caducos [*Baccharis coridifolia* DC.]; ocasionalmente pueden estar acompañados por pelos uniseriados con célula apical flageliforme, pelos uniseriados con pedestal y pelos glandulares biseriados. Hojas sésiles, enteras y revolutas o planas, en apariencia uninervadas, concoloras o discoloras. Capítulos pedunculados, dispuestos en el extremo de ramitas muy breves y/o en la axila de las hojas superiores, formando un racimo folioso; el conjunto de las ramas compone una amplia sinflorescencia paniculiforme; involucros acampanados; receptáculos planos, convexos o cónicos, desprovistos de páleas; proporción de flores carpeladas:estaminadas ca. 1:1. Corola de las flores carpeladas con ápice regularmente 5-dentado; aquenios teretes o ligeramente comprimidos, 5- a 8-costados, con pelos glandulares biseriados a veces acompañados por pelos gemelos, sin papilas, no visibles debajo del involucro a la madurez; cerdas del papus de las flores carpeladas biseriadas, acrescentes, persistentes. Corola de las flores estaminadas con limbo bien diferenciado; estilo con ramas lanceoladas y separadas; cerdas del papus de las flores estaminadas con ápice no ensanchado.

Distribución. *Baccharis* secc. *Coridifoliae* comprende siete especies, propias del sur de Brasil, Bolivia, Paraguay, Uruguay y norte y centro de Argentina (Barroso, 1976; Soria & Zardini, 1995; Giuliano, 2000, 2008; Müller, 2006).

ESPECIES INCLUIDAS

1. Baccharis albolanosa A. S. Oliveira & Deble, Balduinia 9: 4. 2006.

2. Baccharis artemisioides Hook. & Arn. in Hook., J. Bot. (Hooker) 3: 41. 1840.

3. Baccharis coridifolia DC., Prodr. 5: 422. 1836. TIPO: Brasil. Rio Grande do Sul: Feb.–Mar. 1824, *Sellow d1893* [ex Herb. Mus. Imp. Brasiliensis n° 826] (lectotipo, designado por Müller [2006: 273], P no visto).

4. Baccharis erigeroides DC., Prodr. 5: 418. 1836.

5. Baccharis ochracea Spreng., Syst. Veg. (ed. 16) [Sprengel] 3: 460. 1826.

6. Baccharis scabrifolia G. Heiden, Bradea 13(2): 6. 2008.

7. Baccharis suberectifolia A. S. Oliveira-Deble & Deble, Bonplandia 17: 22. 2008.

Las especies de la sección *Coridifoliae* se diferencian de la sección *Tarchonanthoides* (Heering) Cuatrec. (integrada por su especie tipo, *Baccharis tarchonanthoides* DC., y *B. lychnophora* Gardner) por las hojas sésiles en apariencia uninervadas (vs. hojas pecioladas retinervadas en sección *Tarchonanthoides* (Heering) Cuatrec.) y las cerdas del papus de las flores carpeladas biseriadas acrescentes (vs. cerdas del papus uniseriadas no acrescentes). Anteriormente fueron incluidas en la sección *Paniculatae* (Giuliano, 2001), por la presencia de hojas lineares en apariencia uninervadas y la disposición de los capítulos en sinflorescencias paniculiformes. No obstante, esta última pertenece al subgénero *Pteronioides* en virtud de sus flores carpeladas con corolas con ápice truncado a irregularmente denticulado y con una corona de pelos, y aquenios con pelos no glandulares uniseriados a veces acompañados por pelos glandulares biseriados, visibles debajo del involucro a la madurez; en tanto, la sección *Coridifoliae* corresponde al subgénero *Tarchonanthoides* dada la presencia de flores carpeladas con corolas con ápice regularmente 5-dentado, sin corona de pelos, y aquenios con pelos glandulares biseriados a veces acompañados por pelos gemelos, no visibles debajo del involucro.

Si bien Cuatrecasas (1967) designó a *Baccharis artemisioides* como especie lectotipo del subgénero y la sección *Tarchonanthoides*, debe considerarse como especie tipo de este taxón a *B. tarchonanthoides* (McNeill et al., 2006: Art. 22.6), la cual fue incluida indirectamente en el subgénero por Heering (1904) en una nota de pie de página cuya referencia está a continuación del nombre del subgénero (Baker l.c. t. 20, lámina correspondiente a *B. tarchonanthoides*), evidenciando así que el nombre subgenérico deriva del de esta especie.

Nuevas Secciones no Asignables a Rango de Subgénero en *Baccharis*

Las secciones que se describen a continuación no se corresponden con ninguno de los subgéneros establecidos; probablemente constituyan subgéneros en sí mismas, pero ello debe ser corroborado mediante estudios filogenéticos.

Baccharis secc. **Arenariae** Giuliano, sect. nov. TIPO: *Baccharis arenaria* Baker.

Haec sectio sectioni *Angustifoliis* Baker subgeneris *Pteronioidum* Heering capitulis pedunculatis solitariis vel paucis ad apicem ramorum dispositis similis, sed ab ea indumento ex trichomatibus glandulosis eglandulosisque in caespites aggregatis constanti, foliis trinerviis, ratione florum carpellatorum cum staminatis ca. 4:1 et acheniis glabris subter involucrum ad maturitatem non visibilibus differt.

Arbustos erectos; indumento constituido por diminutos pelos glandulares biseriados y pelos no glandulares uniseriados con célula apical breve y de ápice redondeado, agrupados en nidos (a veces los nidos presentan sólo pelos glandulares o pelos no glandulares). Hojas sésiles, enteras o con 1 a 6 dientes pequeños a cada lado en la mitad superior del margen, trinervadas. Capítulos pedunculados, solitarios o agrupados en número de 2 ó 3 en el ápice de los tallos y de ramas laterales breves; involucros hemisféricos; receptáculos planos o levemente convexos, desprovistos de páleas; proporción de flores carpeladas:estaminadas ca. 4:1. Corola de las flores carpeladas con ápice truncado y con una corona de pelos; aquenios 5-costados, glabros, sin papilas, no visibles debajo del involucro a la madurez; cerdas del papus de las flores carpeladas dispuestas en 1 serie, acrescentes, persistentes. Corola de las flores estaminadas con limbo bien diferenciado; estilo con ramas lanceoladas y separadas; cerdas del papus de las flores estaminadas con ápice ensanchado.

Distribución. *Baccharis* secc. *Arenariae* comprende una sola especie, propia del sur de Brasil, Uruguay y nordeste de Argentina (Cabrera, 1974; Barroso, 1976; Giuliano, 2000, 2008).

ESPECIE INCLUIDA

1. **Baccharis arenaria** Baker, Fl. Bras. [Martius] 6(3): 62. 1882. TIPO: Uruguay. Río Santa Lucía, 1 Nov. 1867, *Gibert 115* (lectotipo, aquí designado, K no visto, K000221999 imagen digitalizada!).

Observaciones. Este espécimen es seleccionado como lectotipo porque coincide exactamente con la localidad típica consignada por Baker; el sintipo *King 155* (K) fue colectado en Montevideo, mientras que el labelo de los restantes sintipos, *Sello 588* (B†) y *Sello 2130* (K), consigna "Brasilia". En la misma cartulina donde está montado el espécimen *Gibert 115*, K000221999, existe otro ejemplar *Gibert 115* (K000222000), cuyo labelo consigna "Bois du [Ponds?]", Nov. 1864; en otra cartulina está montado otro espécimen *Gibert 115* (K000222001), "Bois de la Banda Oriental", jul. 1868. Barroso (1976) designó el espécimen *Sello 588* como lectotipo (sub holotipo); no obstante, esa elección es aquí rechazada porque, como se mencionó anteriormente, su labelo consigna "Brasilia", mientras que Baker no citó explícitamente a dicho país en el protólogo; en cambio, el espécimen *Gibert*

115, K000221999, aquí designado como lectotipo, procede de la localidad típica en Uruguay.

Esta especie fue anteriormente ubicada en la sección *Angustifoliae* Baker (Giuliano, 2001), por presentar capítulos pedunculados solitarios o poco agrupados en el ápice de las ramas; no obstante, este taxón debe reservarse para incluir a su especie lectotipo, *Baccharis ulicina* Hook. & Arn., y especies afines (*B. darwinii* Hook. & Arn., *B. melanopotamica* Speg., *B. petrophila* R. E. Fr.), correspondiente al subgénero *Pteronioides*. *Baccharis arenaria* se diferencia de dicha sección por el indumento de nidos pilosos (vs. pelos no agrupados en nidos en sección *Angustifoliae*), las hojas trinervadas (vs. en apariencia uninervadas), la proporción de flores carpeladas:estaminadas ca. 4:1 (vs. ca. 1:1), y los aquenios glabros no visibles debajo del involucro a la madurez (vs. aquenios con pelos uniseriados visibles debajo del involucro).

Müller (2006) incluyó a *Baccharis arenaria* en el grupo informal de *B. juncea* (Lehm.) Desf. junto con *B. acaulis* (Wedd. ex R. E. Fr.) Cabrera y *B. nivalis* (Wedd.) Sch. Bip. ex Phil. No obstante, existen diferencias de importancia entre estas especies; en efecto, *B. arenaria* se diferencia de *B. juncea* por la presencia de hábito arbustivo (vs. hábito herbáceo), pelos agrupados en nidos (vs. pelos no agrupados en nidos), hojas trinervadas (vs. hojas en apariencia uninervadas), proporción de flores carpeladas:estaminadas ca. 4:1 (vs. 6:1 a 8:1), corolas de las flores carpeladas con una corona de numerosos pelos en el ápice (vs. corolas con pelos apicales aislados) y cerdas del papus de las flores carpeladas dispuestas en una serie, moderadamente acrescentes (vs. cerdas en una, dos o más series, notablemente acrescentes); *B. arenaria* se diferencia de *B. acaulis* por presentar hábito arbustivo no pigmeo (vs. hábito herbáceo pigmeo), pelos agrupados en nidos (vs. pelos no agrupados en nidos), hojas trinervadas no dispuestas en rosetas (vs. hojas en apariencia uninervadas dispuestas en rosetas), capítulos pedunculados (vs. capítulos sésiles), involucros hemisféricos (vs. involucros acampanados), receptáculos desprovistos de páleas (vs. receptáculos de los capítulos carpelados con páleas), proporción de flores carpeladas:estaminadas ca. 4:1 (vs. ca. 2:1), corolas de las flores carpeladas con una corona de pelos en el ápice (vs. corolas con pelos apicales aislados) y cerdas del papus de las flores estaminadas con ápice ensanchado (vs. cerdas con ápice no ensanchado); *B. arenaria* se diferencia de *B. nivalis* por la presencia de hábito arbustivo (vs. hábito herbáceo), pelos agrupados en nidos (vs. pelos no agrupados en nidos), hojas trinervadas (vs. hojas en apariencia uninervadas), involucros hemisféricos (vs. involucros acampanados), proporción de flores carpeladas:estaminadas ca. 4:1 (vs. ca. 1:1), aquenios teretes glabros (vs. aquenios leve o marcadamente comprimidos, con pelos gemelos muy largos y densos) y cerdas del papus de las flores carpeladas dispuestas en una serie (vs. cerdas dispuestas en dos o más series). Por otra parte, *B. acaulis* se diferencia de *B. juncea* por la presencia de hábito pigmeo (vs. hábito no pigmeo), hojas dispuestas en rosetas (vs. hojas no dispuestas en rosetas), capítulos sésiles (vs. capítulos pedunculados), involucros acampanados (vs. involucros hemisféricos), receptáculos de los capítulos carpelados con páleas (vs. receptáculos desprovistos de páleas) y proporción de flores carpeladas:estaminadas ca. 2:1 (vs. 6:1 a 8:1). Debido a las marcadas diferencias entre estas cuatro especies, se considera aquí que las mismas deben ser incluidas en distintas secciones; así, *B. acaulis* y *B. juncea* pertenecen respectivamente a las rehabilitadas secciones *Psila* (Phil.) Cuatrec. y *Stephananthus* (Lehm.) Cuatrec., mientras que para *B. nivalis* se propone la nueva sección *Palenia* (véase más adelante).

Baccharis secc. **Rodriguezianae** Giuliano, sect. nov.
TIPO: *Baccharis rodriguezii* Ariza.

A ceteris sectionibus generis *Baccharidis* L. trichomatibus conicis 1- ad 4-cellularibus, foliis ut videtur uninerviis, capitulis in racemos foliosos dispositis, ratione florum carpellatorum cum staminatis ca. 1:2, acheniis valde compressis 3- vel 4-costatis et pappo florum carpellatorum uniseriato non accrescenti conjunctim praesentibus differt.

Arbustos erectos; indumento constituido por pelos no glandulares uniseriados cónicos con pedestal, con cuerpo de 1 a 4 células, pelos uniseriados con célula apical flageliforme y pelos glandulares biseriados, no agrupados en nidos. Hojas sésiles, enteras, en apariencia uninervadas. Capítulos pedunculados, dispuestos en la axila de las hojas superiores formando un racimo folioso; involucros acampanados; receptáculos convexos o cónicos, desprovistos de páleas; proporción de flores carpeladas:estaminadas ca. 1:2. Corola de las flores carpeladas con ápice regularmente dentado; aquenios marcadamente comprimidos, 3- ó 4-costados, con pelos gemelos y pelos glandulares biseriados (estos últimos en la región apical), sin papilas, no visibles debajo del involucro a la madurez; cerdas del papus de las flores carpeladas uniseriadas, no acrescentes, persistentes. Corola de las flores estaminadas con limbo bien diferenciado del tubo; estilo con ramas lanceoladas y separadas; cerdas del papus de las flores estaminadas con ápice regularmente denticulado, no ensanchado.

Distribución. *Baccharis* secc. *Rodriguezianae* comprende una sola especie, endémica de la Sierra de los Quilmes en las provincias de Salta y Tucumán, Argentina (Giuliano, 2000, 2008).

ESPECIE INCLUIDA

1. Baccharis rodriguezii Ariza, Kurtziana 7: 190, fig. 2. 1973. TIPO: Argentina. Salta: Dpto. Cafayate, El Alisal, cerro del Cajón, 7 abr. 1914, *Rodríguez 1430* (holotipo, LIL no visto; isotipo, LP!).

Esta especie es única en el género *Baccharis* en virtud de la combinación de los siguientes caracteres: indumento de pelos cónicos 1 a 4 celulares, hojas en apariencia uninervadas, capítulos dispuestos en racimos foliosos, proporción de flores carpeladas:estaminadas ca. 1:2, aquenios marcadamente comprimidos 3- ó 4-costados y papus de las flores carpeladas uniseriado y no acrescente. Previamente fue ubicada en la sección *Pseudobaccharis* (Cabrera) Cuatrec. (Giuliano, 2001), debido a las hojas en apariencia uninervadas y los capítulos dispuestos en racimos; no obstante, la sección *Pseudobaccharis* debe reservarse para incluir a su especie tipo, *B. spartioides* (Hook. & Arn. ex DC.) J. Rémy, correspondiente al subgénero *Molina*.

Con respecto a las restantes cuatro especies previamente incluidas en la sección *Pseudobaccharis* (Giuliano, 2001), *Baccharis grisebachii* Hieron. y *B. polifolia* Griseb. corresponden a la sección *Subliguliflorae* Giuliano—en concordancia con el criterio de Müller (2006), quien reunió estas especies en el grupo informal de *B. polifolia*—mientras que *B. boliviensis* (Wedd.) Cabrera pertenece a la sección *Heterothalamus* (Less.) Giuliano (véase más adelante); en tanto, para *B. thymifolia* Hook. & Arn. se propone una nueva sección (véase más adelante).

Baccharis secc. **Tenellae** Giuliano, sect. nov. TIPO: *Baccharis tenella* Hook. & Arn.

Haec sectio sectioni *Angustifoliis* Baker subgeneris *Pteronioidum* Heering foliis linearibus ut videtur uninerviis et capitulis pedunculatis solitariis vel paucis ad apicem ramorum dispositis similis, sed ab ea habitu herbaceo, trichomatibus uniseriatis 2-cellularibus cellula apicali longissima flagelliformi, ratione florum carpellatorum cum staminatis ca. 2:1, receptaculis capitulorum carpellatorum paleaceis et acheniis trichomatibus geminis indutis differt.

Hierbas perennes, con tallos decumbentes o ascendentes; indumento constituido por pelos no glandulares uniseriados 2-celulares, con célula basal rectangular y célula apical muy larga y flageliforme, no agrupados en nidos; estos pelos se presentan densamente dispuestos formando una pubescencia lanuginosa. Hojas sésiles, enteras, en apariencia uninervadas. Capítulos pedunculados, solitarios en el ápice de las ramitas; involucros de los capítulos carpelados hemisféricos, los de los estaminados acampanados; receptáculos planos o levemente convexos, los de los capítulos carpelados provistos de páleas; proporción de flores carpeladas:estaminadas ca. 2:1. Corola de las flores carpeladas con ápice irregularmente denticulado, con pelos en el ápice de los dientes; aquenios teretes, 8- a 10-costados, con pelos gemelos, sin papilas, ligeramente visibles debajo del involucro a la madurez; cerdas del papus de las flores carpeladas dispuestas en 2 o más series, acrescentes, persistentes. Corola de las flores estaminadas con limbo bien diferenciado; estilo con ramas lanceoladas y separadas; cerdas del papus de las flores estaminadas con ápice no ensanchado.

Distribución. *Baccharis* secc. *Tenellae* comprende una sola especie, endémica del centro y sur de Argentina (Cabrera, 1971; Giuliano, 2000, 2008).

ESPECIE INCLUIDA

1. Baccharis tenella Hook. & Arn. in Hook., J. Bot. (Hooker) 3: 42. 1840. *Heterothalamus tenellus* (Hook. & Arn.) Kuntze, Revis. Gen. Pl. 3(3): 158. 1898. *Pseudobaccharis tenella* (Hook. & Arn.) Cabrera, Notas Mus. La Plata, Bot. 9: 248. 1944. *Psila tenella* (Hook. & Arn.) Cabrera, Bol. Soc. Argent. Bot. 5: 210. 1955. TIPO: Argentina. Buenos Aires: Bahía Blanca, Arroyo Napostá, s.d., *Tweedie 40* (holotipo, K no visto, K000222094 imagen digitalizada!).

Esta especie fue anteriormente ubicada en la sección *Angustifoliae* (Giuliano, 2001, 2005), por presentar hojas lineares en apariencia uninervadas y capítulos pedunculados solitarios o poco agrupados en el ápice de las ramas; no obstante, se diferencia por presentar hábito herbáceo (vs. hábito subarbustivo en sección *Angustifoliae*), indumento sólo de pelos uniseriados 2-celulares con célula apical muy larga y flageliforme (vs. pelos uniseriados incurvados y pelos uniseriados ramificados), proporción de flores carpeladas:estaminadas ca. 2:1 (vs. ca. 1:1), páleas en los receptáculos de los capítulos carpelados (vs. páleas ausentes) y aquenios con pelos gemelos (vs. aquenios con pelos uniseriados).

Baccharis secc. **Thymifoliae** Giuliano, sect. nov. TIPO: *Baccharis thymifolia* Hook. & Arn.

A ceteris sectionibus generis *Baccharidis* L. trichomatibus eglandulosis cellulis subapicalibus valde dilatatis atque cellula apicali ramosa et corollis florum carpellatorum apice dentibus rotundatis differt.

Arbustos erectos; indumento constituido por pelos no glandulares uniseriados con células subapicales notoriamente ensanchadas y célula apical ramificada, con 1 ó 2 ramas principales y ramificaciones secundarias, y pelos glandulares biseriados, solitarios o agrupados en nidos de pocos pelos. Hojas sésiles, enteras, en apariencia uninervadas. Capítulos pedunculados, dispuestos en la axila de las hojas superiores formando un racimo folioso; involucros acampanados; receptáculos cónicos, desprovistos de páleas; proporción de flores carpeladas:estaminadas ca. 1:1. Corola de las flores carpeladas con ápice regularmente 5-dentado, con dientes anchos y redondeados; aquenios marcadamente comprimidos, 3- ó 4-costados, con pelos gemelos y pelos glandulares biseriados, sin papilas, no visibles debajo del involucro a la madurez; cerdas del papus de las flores carpeladas uniseriadas, no acrescentes, persistentes. Corola de las flores estaminadas con limbo bien diferenciado; estilo con ramas lanceoladas y separadas; cerdas del papus de las flores estaminadas con ápice regularmente denticulado.

Distribución. *Baccharis* secc. *Thymifoliae* comprende una sola especie, endémica de la provincia de Mendoza en Argentina (Giuliano, 2000, 2008).

ESPECIE INCLUIDA

1. **Baccharis thymifolia** Hook. & Arn., J. Bot. (Hooker) 3: 38. 1840. TIPO: Argentina. Cienega de las Arrojas, Andes of Mendoza, s.d., *Gillies 166* (holotipo, K no visto, K000222096 imagen digitalizada!).

Esta especie es única en el género *Baccharis* en virtud de los pelos no glandulares con células subapicales notoriamente ensanchadas y célula apical ramificada, y las corolas de las flores carpeladas con ápice con dientes redondeados; asimismo son notables los aquenios marcadamente comprimidos 3- ó 4-costados con el papus con cerdas uniseriadas muy breves. Previamente fue clasificada en la sección *Pseudobaccharis* (Giuliano, 2001), por la presencia de hojas en apariencia uninervadas y capítulos dispuestos en racimos; esta sección, como ya ha sido mencionado, debe reservarse para incluir a su especie tipo, *B. spartioides*, correspondiente al subgénero *Molina*.

NUEVAS COMBINACIONES EN *BACCHARIS*

Baccharis secc. **Heterothalamus** (Less.) Giuliano, comb. et stat. nov. Basiónimo: *Heterothalamus* Less., Linnaea 5: 145. 1830. TIPO: *Baccharis aliena* (Spreng.) Joch. Müller [≡ *Marshallia aliena* Spreng.; ≡ *Heterothalamus alienus* (Spreng.) Kuntze].

Heterothalamulopsis Deble, A. S. Oliveira & Marchiori, Ci. Florest. 14: 1. 2004. TIPO: *Heterothalamus wagenitzii* F. H. Hellw. [≡ *Heterothalamulopsis wagenitzii* (F. H. Hellw.) Deble, A. S. Oliveira & Marchiori; ≡ *Baccharis wagenitzii* (F. H. Hellw.) Joch. Müller].

Tradicionalmente, el género *Heterothalamus* Less. comprendía dos especies polígamo-dioicas (*H. alienus* (Spreng.) Kuntze y *H. psiadioides* Less.), a las que posteriormente se agregó una tercera (*H. rupestris* Deble, A. S. Oliveira & Marchiori); sin embargo, recientemente se describió una especie dioica (*H. wagenitzii* F. H. Hellw.). Asimismo, *Baccharis boliviensis* presenta afinidades con estas especies (cf. Hellwig, 2003; Müller, 2006); de esta manera, resulta imposible diferenciar los géneros *Baccharis* y *Heterothalamus*, por lo que se acepta el criterio de Müller (2006) de incluir el segundo en el primero, considerándolo aquí con status de sección. El género *Heterothalamulopsis*, creado para incluir a *Heterothalamus wagenitzii* (Deble et al., 2004), es en consecuencia considerado aquí como sinónimo de la nueva sección *Heterothalamus*.

Los caracteres que definen a la sección *Heterothalamus* son los siguientes: receptáculos de los capítulos carpelados provistos de páleas, corolas de las flores carpeladas muy breves (su longitud es aproximadamente la misma de la de los aquenios) con ápice cortamente ligulado, estilos de las flores carpeladas apenas exsertos, aquenios usualmente comprimidos 2- a 5-costados y cerdas del papus de las flores carpeladas uniseriadas, no acrescentes y caducas.

Müller (2006) incluyó a las especies de la sección *Heterothalamus*—bajo el grupo informal *Heterothalamus*—en el subgénero *Molina*. Sin embargo, la mayoría de los caracteres propios de la sección *Heterothalamus* son ocasionales o de hecho no se encuentran en dicho subgénero: en *Molina*, los receptáculos de los capítulos carpelados presentan páleas sólo en las secciones *Pseudobaccharis* y *Trinervatae*; la longitud de las corolas de las flores carpeladas es mayor a la de los aquenios, y el ápice de las mismas es brevemente ligulado sólo en las secciones *Caulopterae* y *Pseudobaccharis*; los estilos de las flores carpeladas son exsertos; los aquenios generalmente son teretes 5- a 8-costados, y las cerdas

del papus de las flores carpeladas, si bien son uniseriadas, son ligera a moderadamente acrescentes y persistentes. En consecuencia, resultaría necesario efectuar estudios filogenéticos para establecer con precisión la ubicación sistemática de la sección *Heterothalamus* y de la afín sección *Subliguliflorae*, asimismo incluida por Müller (2006, bajo el grupo informal de *Baccharis polifolia*) en el subgénero *Molina*.

Distribución. *Baccharis* secc. *Heterothalamus* comprende cinco especies propias del sur de Brasil, Uruguay y centro de Argentina y la región andina desde el sur de Perú hasta el norte de Chile y el noroeste de Argentina (Barroso, 1976; Giuliano, 2000, 2008; Müller, 2006).

ESPECIES INCLUIDAS

1. Baccharis aliena (Spreng.) Joch. Müller, Syst. Bot. Monogr. 76: 305. 2006. Basiónimo: *Marshallia aliena* Spreng., Syst. Veg. [Sprengel] (ed. 16) 3: 446. 1826. *Heterothalamus alienus* (Spreng.) Kuntze, Revis. Gen. Pl. 3(3): 158. 1898. TIPO: Uruguay. Montevideo, s.d., *Sello s.n.* (holotipo, P foto en LP!).

Observaciones. Malagarriga Heras (1957) y Barroso (1976) consideran a Rio Grande do Sul, Brasil, como la localidad típica.

2. Baccharis boliviensis (Wedd.) Cabrera, Bol. Soc. Argent. Bot. 16: 256. 1975.

3. Baccharis hyemalis Deble, Balduinia 9: 20. 2006.

4. Baccharis psiadioides (Less.) Joch. Müller, Syst. Bot. Monogr. 76: 306. 2006.

5. Baccharis wagenitzii (F. H. Hellw.) Joch. Müller, Syst. Bot. Monogr. 76: 306. 2006.

Baccharis secc. **Icma** (Phil.) Giuliano, comb. et stat. nov. Basiónimo: *Icma* Phil., Anales Univ. Chile 41: 740. 1872. TIPO: *Icma involucrata* Phil. [= *Baccharis gilliesii* A. Gray].

Esta sección pertenece al subgénero *Baccharis* en virtud de los siguientes caracteres: corola de las flores carpeladas con ápice 5-dentado; aquenios teretes, 10- a 12-costados, glabros, sin papilas, no visibles debajo del involucro a la madurez; cerdas del papus de las flores carpeladas dispuestas en dos series, acrescentes, caducas; corola de las flores estaminadas con limbo gradualmente diferenciado del tubo; ápice del estilo obtrulado, con ramas breves y mayormente adheridas entre sí; cerdas del papus de las flores estaminadas con ápice ensanchado.

Dentro del subgénero *Baccharis*, la seccción *Icma* (Phil.) Giuliano se distingue por presentar los siguientes caracteres: subarbustos erectos; pelos no glandulares de los nidos con célula apical brevemente flagelada; capítulos sésiles, solitarios en el extremo de las ramas y rodeados por un falso involucro de pequeñas hojas, a veces agrupados formando una sinflorescencia corimbiforme; proporción de flores carpeladas:estaminadas ca. 2:1.

Distribución. Comprende una sola especie, endémica de Argentina (Cabrera, 1974; Giuliano, 2000, 2008).

ESPECIE INCLUIDA

1. Baccharis gilliesii A. Gray, Proc. Amer. Acad. Arts, 5: 123. 1860–1862.

Icma involucrata Phil., Anales Univ. Chile 41: 741. 1872. TIPO: Argentina. Mendoza, s.d., *R. A. Philippi s.n.* (holotipo, SGO no visto; isotipos, CORD foto en SI!, G foto serie F.M. n° 28510 en LP!).

Baccharis gilliesii fue anteriormente incluida en la sección *Cuneifoliae* (Giuliano, 2001), por poseer capítulos sésiles solitarios en el ápice de las ramas, cada uno rodeado por un falso involucro de pequeñas hojas, pero se diferencia de este taxón por presentar pelos uniseriados de los nidos pilosos con célula apical brevemente flagelada y con paredes delgadas (vs. triangular y con paredes gruesas en sección *Cuneifoliae*) y sinflorescencia corimbiforme (vs. racemiforme).

Baccharis secc. **Palenia** (Phil.) Giuliano, comb. et stat. nov. Basiónimo: *Palenia* Phil., Anales Univ. Chile 90: 7. 1895. TIPO: *Palenia delfinii* Phil. [= *Baccharis nivalis* (Wedd.) Sch. Bip. ex Phil.].

La única especie incluida en esta sección presenta hábito herbáceo, con tallos decumbentes o ascendentes; el indumento está constituido por diminutos pelos no glandulares uniseriados con cuerpo de 4 ó 5 células rectangulares anchas y célula apical breve y de ápice obtuso o redondeado, y pelos glandulares biseriados, no agrupados en nidos, ubicados sobre las nervaduras de las hojas. Las hojas son sésiles, enteras, en apariencia uninervadas. Los capítulos son largamente pedunculados, solitarios en el ápice de las ramitas; los involucros son acampanados; los receptáculos convexos, desprovistos de páleas; la proporción de flores carpeladas:estaminadas es ca. 1:1. La corola de las flores carpeladas presenta ápice

truncado con una corona de pelos; los aquenios son leve o marcadamente comprimidos, 5-costados, con pelos gemelos muy largos y densos, sin papilas, ligeramente visibles debajo del involucro a la madurez; las cerdas del papus de las flores carpeladas están dispuestas en 2 o más series, acrescentes, persistentes. La corola de las flores estaminadas presenta limbo bien diferenciado; el estilo posee ramas lanceoladas y separadas; las cerdas del papus de las flores estaminadas tienen el ápice ensanchado. Debido a la combinación de estos caracteres, no es posible asignar a la sección *Palenia* (Phil.) Giuliano a alguno de los subgéneros ya establecidos.

Distribución. Comprende una sola especie, propia del sur de Chile y Argentina (Cabrera, 1971; Giuliano, 2000, 2008).

ESPECIE INCLUIDA

1. Baccharis nivalis (Wedd.) Sch. Bip. ex Phil., Anales Univ. Chile 87: 705. 1894. Basiónimo: *Heterothalamus nivalis* Wedd., Chlor. Andina 1(4–6): 179. 1855 [1856].

Palenia delfinii Phil., Anales Univ. Chile 90: 7. 1895. TIPO: Chile. Río Palena, ene.–feb. 1887, *Delfin s.n.* (holotipo, SGO no visto, imagen digitalizada!).

Esta especie fue anteriormente ubicada en la sección *Angustifoliae* (Giuliano, 2001, 2005), por presentar hojas lineares en apariencia uninervadas y capítulos pedunculados solitarios o poco agrupados en el ápice de las ramas; no obstante, se diferencia por presentar hábito herbáceo (vs. subarbustivo en sección *Angustifoliae*), indumento de pelos uniseriados rectos no ramificados y pelos glandulares biseriados (vs. pelos uniseriados incurvados y pelos uniseriados rectos ramificados) y aquenios con pelos gemelos muy largos y densos (vs. aquenios con pelos uniseriados laxos).

Hellwig (1996) incluyó a *Baccharis nivalis* en el género rehabilitado *Stephananthus* Lehm. junto con *B. acaulis* y *B. juncea*; Müller (2006), como ya fue mencionado anteriormente, reunió a estas especies en el grupo informal de *B. juncea* dentro del género *Baccharis*, incluyendo además a *B. arenaria*. No obstante, *B. nivalis* se diferencia de *B. acaulis* por presentar hojas no dispuestas en rosetas, no abrazadoras en la base (vs. hojas dispuestas en rosetas, abrazadoras en la base), capítulos pedunculados (vs. capítulos sésiles), proporción de flores carpeladas:estaminadas ca. 1:1 (vs. ca. 2:1), corolas de las flores carpeladas con una corona de pelos en el ápice (vs. corolas con pelos apicales aislados), receptáculos desprovistos de páleas (vs. receptáculos de los capítulos carpelados con páleas), aquenios con pelos gemelos muy largos y densos (vs. aquenios glabros) y cerdas del papus de las flores estaminadas con ápice ensanchado (vs. cerdas con ápice no ensanchado); *B. nivalis* se diferencia de *B. juncea* por la presencia de involucros acampanados (vs. involucros hemisféricos), proporción de flores carpeladas: estaminadas ca. 1:1 (vs. 6:1 a 8:1), corolas de las flores carpeladas con una corona de pelos en el ápice (vs. corolas con pelos apicales aislados), aquenios leve o marcadamente comprimidos, con pelos gemelos muy largos y densos (vs. aquenios teretes glabros) y cerdas del papus de las flores carpeladas moderadamente acrescentes (vs. cerdas notablemente acrescentes); en tanto, las diferencias entre *B. nivalis* y *B. arenaria* ya fueron analizadas en la discusión de la nueva sección *Arenariae*. Las considerables diferencias entre estas cuatro especies justifican su inclusión en secciones independientes.

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Apéndice 1. Orden alfabético de especies de *Baccharis* previamente clasificadas (Giuliano, 2001) y aquí reubicadas en otras secciones.

Especies de *Baccharis*	Secciones en las que fueron clasificadas previamente (Giuliano, 2001)	Secciones en las que son reubicadas
B. acaulis (Wedd. ex R.E. Fr.) Cabrera	secc. *Angustifoliae* Baker	secc. *Psila* (Phil.) Cuatrec.
B. albida Hook. & Arn.	secc. *Molina* (Pers.) Cuatrec.	secc. *Albidae* Giuliano
B. anomala DC.	secc. *Trinervatae* DC.	secc. *Scandentes* Cuatrec.
B. arenaria Baker	secc. *Angustifoliae* Baker	secc. *Arenariae* Giuliano
B. artemisioides Hook. & Arn.	secc. *Paniculatae* Heering	secc. *Coridifoliae* Giuliano
B. boliviensis (Wedd.) Cabrera	secc. *Pseudobaccharis* (Cabrera) Cuatrec.	secc. *Heterothalamus* (Less.) Giuliano
B. caespitosa (Ruiz & Pav.) Pers.	secc. *Cuneifoliae* DC.	secc. *Caespitosae* Giuliano
B. caprariifolia DC.	secc. *Discolores* DC.	secc. *Racemosae* Ariza
B. coridifolia DC.	secc. *Paniculatae* Heering	secc. *Coridifoliae* Giuliano
B. divaricata Hauman	secc. *Baccharis*	secc. *Divaricatae* Giuliano
B. dracunculifolia DC.	secc. *Discolores* DC.	secc. *Racemosae* Ariza
B. effusa Griseb.	secc. *Paniculatae* Heering	secc. *Effusae* Giuliano
B. elaeagnoides Steud. ex Baker	secc. *Nitidae* Cuatrec.	secc. *Racemosae* Ariza
B. famatinensis Ariza	secc. *Baccharis*	secc. *Tucumanenses* Giuliano
B. frenguellii Cabrera	secc. *Discolores* DC.	secc. *Frenguellianae* Giuliano
B. gilliesii A. Gray	secc. *Cuneifoliae* DC.	secc. *Icma* (Phil.) Giuliano
B. glutinosa Pers. (sub *B. pingraea* DC.)	secc. *Molina* (Pers.) Cuatrec.	secc. *Baccharidastrum* (Cabrera) G. L. Nesom
B. grisebachii Hieron.	secc. *Pseudobaccharis* (Cabrera) Cuatrec.	secc. *Subliguliflorae* Giuliano
B. juncea (Lehm.) Desf.	secc. *Angustifoliae* Baker	secc. *Stephananthus* (Lehm.) Cuatrec.
B. kurtziana Ariza	secc. *Cuneifoliae* DC.	secc. *Tucumanenses* Giuliano
B. lilloi Heering	secc. *Aristidentes* G. L. Nesom	secc. *Lilloanae* Giuliano
B. megapotamica Spreng.	secc. *Discolores* DC.	secc. *Megapotamicae* Giuliano
B. multiflosculosa Heering (sub *B. pulchella* Sch. Bip. ex Griseb.)	secc. *Aristidentes* G. L. Nesom	secc. *Lilloanae* Giuliano
B. nivalis (Wedd.) Sch. Bip. ex Phil.	secc. *Angustifoliae* Baker	secc. *Palenia* (Phil.) Giuliano
B. ochracea Spreng.	secc. *Paniculatae* Heering	secc. *Coridifoliae* Giuliano
B. oxyodonta DC.	secc. *Trinervatae* DC.	secc. *Molina* (Pers.) Cuatrec.
B. polifolia Griseb.	secc. *Pseudobaccharis* (Cabrera) Cuatrec.	secc. *Subliguliflorae* Giuliano
B. polygama Ariza	secc. *Aristidentes* G. L. Nesom	secc. *Molina* (Pers.) Cuatrec.
B. pulchella Sch. Bip. ex Griseb.	secc. *Aristidentes* G. L. Nesom	secc. *Tubulatae* Cuatrec.
B. punctulata DC.	secc. *Trinervatae* DC.	secc. *Molina* (Pers.) Cuatrec.
B. racemosa (Ruiz & Pav.) DC.	secc. *Aristidentes* G. L. Nesom	secc. *Australes* Giuliano
B. rodriguezii Ariza	secc. *Pseudobaccharis* (Cabrera) Cuatrec.	secc. *Rodriguezianae* Giuliano
B. rupestris Heering	secc. *Cuneifoliae* DC.	secc. *Tucumanenses* Giuliano
B. santelicis Phil. (sub *B. polycephala* Wedd.)	secc. *Cuneifoliae* DC.	secc. *Caespitosae* Giuliano
B. semiserrata DC.	secc. *Nitidae* Cuatrec.	secc. *Racemosae* Ariza
B. spicata (Lam.) Baill.	secc. *Baccharis*	secc. *Spicatae* Giuliano
B. stenophylla Ariza	secc. *Molina* (Pers.) Cuatrec.	secc. *Baccharidastrum* (Cabrera) G. L. Nesom
B. tandilensis Speg. (sub *B. dracunculifolia* DC.)	secc. *Discolores* DC.	secc. *Racemosae* Ariza
B. tenella Hook. & Arn.	secc. *Angustifoliae* Baker	secc. *Tenellae* Giuliano
B. thymifolia Hook. & Arn.	secc. *Pseudobaccharis* (Cabrera) Cuatrec.	secc. *Thymifoliae* Giuliano
B. tola Phil. (sub *B. incarum* (Wedd.) Perkins)	secc. *Cuneifoliae* DC.	secc. *Caespitosae* Giuliano
B. triangularis Hauman	secc. *Cuneifoliae* DC.	secc. *Caulopterae* DC.
B. tucumanensis Hook. & Arn.	secc. *Baccharis*	secc. *Tucumanenses* Giuliano

AN EVALUATION OF CLASSIFICATION BY CUTICULAR CHARACTERS OF THE LAURACEAE: A COMPARISON TO MOLECULAR PHYLOGENY[1]

Sachiko Nishida[2] *and Henk van der Werff*[3]

Abstract

Cuticular characters are epidermal or stomatal characters and are often used in the taxonomy and classification of fossil or extant Lauraceae. However, there is no consensus on their usefulness, especially as to which characters take priority and at which taxonomic level. This study compared the cuticular characters of species within the Neotropical genera of the *Ocotea* Aubl. complex to the reported molecular phylogeny. Species of the following genera are included in this study: *Aiouea* Aubl., *Aniba* Aubl., *Dicypellium* Nees & Mart., *Endlicheria* Nees, *Kubitzkia* van der Werff, *Licaria* Aubl., *Nectandra* Rol. ex Rottb., *Ocotea*, *Paraia* Rohwer, H. G. Richt. & van der Werff, *Pleurothyrium* Nees, *Rhodostemonodaphne* Rohwer & Kubitzki, *Umbellularia* (Nees) Nutt., and *Urbanodendron* Mez. Species groups based on cuticular characters, especially characters of the stomata, agreed well with the various clades in the molecular phylogeny, but did not agree with species grouped according to the traditional generic concepts. Stomata characters showed little or no variation within the clades found in the molecular phylogeny. Because the number of character states is limited, cuticular features by themselves cannot be used to define genera or clades or will not allow the identification of specimens.

Key words: *Aiouea*, *Aniba*, classification, cuticle, *Dicypellium*, *Endlicheria*, epidermis, *Kubitzkia*, Lauraceae, *Licaria*, *Nectandra*, *Ocotea*, *Paraia*, *Pleurothyrium*, *Rhodostemonodaphne*, stomata, *Umbellularia*, *Urbanodendron*.

The pantropical family Lauraceae, which consists of about 50 genera comprising 2500 to 3000 species, includes major components of tropical forests and many trees of economic importance (van der Werff & Richter, 1996). Taxonomically, the family is a challenging group, mainly due to the difficulty of finding and then identifying flowers (Nishida & van der Werff, 2007). Fruiting samples are relatively easy to collect, but they can be determined to the genus level at best. Additional characters that are easy to assess and independent of flowers or fruits are sorely needed to better understand the family.

Cuticular characters, which are epidermal or stomatal characters remaining on the cuticles, have proved to be of great use, not only in identifying fossil remains of angiosperms but also in studying relationships among extant taxa (Baranova, 1972, 1987, 1992; Stace, 1984; Upchurch, 1984a, 1984b; Yang & Lin, 2005). Since Christophel et al. (1996) first reported their usefulness for the Lauraceae, an increasing number of studies have applied cuticular characters to the identification or classification of extant and fossil taxa of the family (Christophel & Rowett, 1996; Nishida & Christophel, 1999; Nishida & van der Werff, 2007; Carpenter et al., 2010).

However, no consensus has emerged as to the classification utility of the characters, or which ones might take priority or apply at what taxonomic level in classification. Epidermal cell and stomatal complex characters have been equally emphasized in some studies (Christophel et al., 1996; Nishida & Christophel, 1999), whereas stomata were preferred in others (Bandulska, 1926). Some studies have focused on certain cuticular features to determine genera (Bandulska, 1926; Christophel & Rowett, 1996; Christophel et al., 1996), whereas others have used the characters to group within genera (Nishida & van der Werff, 2007). Studies evaluating the usefulness of cuticular characters within the Lauraceae are long overdue.

We focused on the Neotropical genera of the *Ocotea* Aubl. complex and compared cuticular features of each species to the molecular phylogeny determined by Chanderbali et al. (2001). The *Ocotea* complex was strongly supported by the molecular analysis, with *Ocotea* members being widely dispersed. Major genera of the tropical Lauraceae, such

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as *Endlicheria* Nees, *Licaria* Aubl., *Nectandra* Rol. ex Rottb., *Pleurothyrium* Nees, and *Rhodostemonodaphne* Rohwer & Kubitzki, are included within this complex. Chanderbali et al. (2001) sampled only the *Ocotea* complex representatively, within which seemingly natural groups of genera and parts of larger genera were identified. By comparing the relatively well-supported clades of this molecular study and their cuticular features, we investigate to answer the following three questions: (1) Do the cuticular characters vary within the clades recognized in Chanderbali et al. (2001)?; (2) Are cuticular features diagnostic for molecular-based clades?; and (3) Do cuticular features hold promise for characterizing or identifying species or genera? We also discuss whether the species groups based on cuticular characters better agree with the clades in the molecular phylogeny or species grouped according to the traditional generic concepts.

Materials and Methods

Cuticles of 50 Neotropical species from 13 laurel genera (*Aiouea* Aubl., *Aniba* Aubl., *Dicypellium* Nees & Mart., *Endlicheria*, *Kubitzkia* van der Werff, *Licaria*, *Nectandra*, *Ocotea*, *Paraia* Rohwer, H. G. Richt. & van der Werff, *Pleurothyrium*, *Rhodostemonodaphne*, *Umbellularia* (Nees) Nutt., and *Urbanodendron* Mez) were examined. Their phylogenetic relationships as inferred from sequence variations of the nuclear genomes (ITS/5.8S) were identified by Chanderbali et al. (2001). Table 1 lists the sources of plant materials. Leaves were sampled from herbarium specimens at MO, using one leaf sample per species. Specific cuticular characters within a species remain constant (Nishida & Christophel, 1999; Nishida & van der Werff, 2007).

The cuticles studied here were the cuticular membranes of the epidermis or stomatal complex that remained through the preparation, and the cuticular characters described were mostly features of the epidermal cells or stomatal complex whose impressions were preserved in the membrane (Christophel & Rowett, 1996). The examination procedure followed that of Christophel et al. (1996), Nishida and Christophel (1999), and Nishida and van der Werff (2007). Samples (1 × 1 cm) were taken from near the left basal margin (adaxial surface up) of mature leaves. The leaf samples were soaked in 90% ethanol for ca. 18 hr., then placed in a test tube with 2 mL 30% H_2O_2 and 0.5 mL 90% ethanol. The test tubes were heated at 120°C in a heated dry block bath for about 2 hr. When the samples turned yellow, they were placed in 90% ethanol for ca. 10 hr. before rinsing in 2% ammonia (to adjust the pH), and were transferred to a Petri dish with double-distilled water (ddH_2O). The cellular contents of the sample leaves were removed with a fine artist's brush. The cuticles were stained in 0.1% crystal violet for ca. 1 min., then mounted in phenol glycerin jelly on a slide and observed under a light microscope. Feature descriptions followed Wilkinson (1979), Christophel et al. (1996), Nishida and Christophel (1999), or Nishida and van der Werff (2007).

The cuticles were also examined using an SEM. Sample preparation was the same as described above. Samples were dehydrated in a *t*-butanol series, freeze-dried using a JFD-310 (JEOL, Tokyo, Japan) at 8°C, then coated with platinum, and observed under a JSM-6060B microscope (15 kV; JEOL).

Results

Table 2 lists the cuticular characters recognized in this study. Figures 1–3 show representative micrographs of cuticles in major cuticular groupings. All the species examined were hypostomatic. In addition to the absence or presence of stomata, cuticular features of epidermal cells differed within species between the adaxial and abaxial leaf surfaces.

Among the cuticular characters often used in laurel taxonomy (e.g., Christophel & Rowett, 1996; Christophel et al., 1996), anticlinal wall straightness and stomatal features have varied considerably. Periclinal wall ornamentation and anticlinal wall thickness, in contrast, were uniform for most of the species examined, although both features can vary widely and are useful in distinguishing other laurel species (Christophel et al., 1996). The periclinal wall ornamentation of all of the species was smooth, except as seen in the abaxial leaf surfaces of *Pleurothyrium cinereum* van der Werff (wrinkled), *Aniba cinnamomiflora* C. K. Allen (papillose), and *A. panurensis* (Meisn.) Mez (papillose). The anticlinal walls of all of the species were more or less beaded.

Following Wilkinson (1979) and Nishida and Christophel (1999), we classified anticlinal walls into three types: straight to slightly curved (SC); having loose, wide U-shaped curves of shallow amplitude (LC); or having tight U-shaped curves of shallow amplitude (TC). The main difference among these types was the frequency of curves. SC walls showed no obvious wave shape across one side of the cell but only with the walls straight to roundish (Figs. 1D, E, G, H, J, K, M, N; 2G; 3B, D), whereas LC generally had one wave (Figs. 2H, J, K, M, N; 3E) and TC more than two waves per side (Figs. 1A, B; 2A, B, D, E; 3G, H, K, M, N).

Table 1. Specimens examined for Lauraceae in this study. All the samples were taken from the herbarium specimens at MO.

Species	Country	Voucher
Aiouea costaricensis (Mez) Kosterm.	Costa Rica	*Utley 3040*
Aniba cinnamomiflora C. K. Allen	Venezuela	*Liesner 25806*
Aniba excelsa Kosterm.	Guyana	*Chanderbali 245*
Aniba panurensis (Meisn.) Mez	Peru	*Reynel 603*
Dicypellium caryophyllaceum (Mart.) Nees	Brazil	*Prance 25845*
Dicypellium manausense W. A. Rodrigues	Brazil	*Lopes INPA 2206.2023*
Endlicheria chalisea Chanderbali	Guyana	*Clarke 1465*
Endlicheria citriodora van der Werff	Peru	*van der Werff 9991*
Endlicheria punctulata (Mez) C. K. Allen	French Guiana	*Grenand 2870*
Endlicheria reflectens (Nees) Mez	Guyana	*Jansen-Jacobs 5374*
Kubitzkia mezii (Kosterm.) van der Werff	French Guiana	*Mori 25816*
Licaria cannella (Meisn.) Kosterm.	Brazil	*Daly 10218*
Licaria guianensis Aubl.	French Guiana	*Sabatier 3645*
Licaria martiniana (Mez) Kosterm.	Suriname	*Tawjoeran-LBB 11950*
Licaria triandra (Sw.) Kosterm.	Peru	*Vasquez 25139*
Nectandra amazonum Nees	Guyana	*Matchnick 532*
Nectandra coriacea (Sw.) Griseb.	Guatemala	*Contreras 9598*
Nectandra cuspidata Nees & Mart.	Peru	*van der Werff 18485*
Nectandra psammophila Nees & C. Mart.	Brazil	*Belem 3850*
Nectandra purpurea (Ruiz & Pav.) Mez	Peru	*Hodges 79*
Nectandra salicifolia (Kunth) Nees	Belize	*Urban 13*
Nectandra turbacensis (Kunth) Nees	Mexico	*Beaman 5933*
Ocotea botrantha Rohwer	El Salvador	*Monterrosa 214*
Ocotea ceanothifolia (Nees) Mez	French Guiana	*Sabatier 4200*
Ocotea guianensis Aubl.	Suriname	*Schultz-LBB 9378*
Ocotea helicterifolia (Meisn.) Hemsl.	Nicaragua	*Montenegro 1845*
Ocotea heydeana (Mez & Donn. Sm.) Bernardi	Honduras	*Evans 1778*
Ocotea insularis (Meisn.) Mez	Peru	*van der Werff 16354*
Ocotea nigra Benoist	Suriname	*Schultz-LBB 9335*
Ocotea odorifera (Vell.) Rohwer	Brazil	*Klein 13*
Ocotea pauciflora (Nees) Mez	Ecuador	*Palecios 10995*
Ocotea percoriacea Kosterm.	Brazil	*Magalhaes 1078*
Ocotea pulchella (Nees & Mart.) Mez	Brazil	*Silva 1512*
Ocotea quixos (Lam.) Kosterm.	Ecuador	*Ramirez 18*
Ocotea rhynchophylla (Meisn.) Mez	Peru	*Monteagudo 5217*
Ocotea schomburgkiana (Nees) Mez	Venezuela	*Rodriguez 1271*
Ocotea spixiana (Nees) Mez	Brazil	*Magalhaes 217*
Ocotea tomentella Sandwith	French Guiana	*Sabatier 4434*
Ocotea tristis (Nees & Mart.) Mez	Brazil	*Ribas 5081*
Ocotea veraguensis (Meisn.) Mez	El Salvador	*Martinez 595*
Paraia bracteata Rohwer, H. G. Richt. & van der Werff	Brazil	*Silva AS 109*
Pleurothyrium cinereum van der Werff	Ecuador	*Suin 1888*
Pleurothyrium insigne van der Werff	Colombia	*Madriñán 705*
Rhodostemonodaphne crenaticupula Madriñán	Brazil	*Maas 9209*
Rhodostemonodaphne praeclara (Sandwith) Madriñán	Brazil	*Krukoff 5171*
Rhodostemonodaphne recurva van der Werff	Brazil	*Dos Santos 1202.5767*
Rhodostemonodaphne scandens Madriñán	Guyana	*Clarke 7243*
Umbellularia californica (Hook. & Arn.) Nutt.	U.S.A.	*Chanderbali 326*
Urbanodendron bahiense (Meisn.) Rohwer	Brazil	*Martinelli 10019*
Urbanodendron verrucosum (Nees) Mez	Brazil	*Neto 2580*

Three variations of stomatal features occurred among the examined species: lower stomatal ledge shape, surface appearance of the stomata observed via SEM, and evenness of the shape and size of the subsidiary cells.

The stomatal ledges were the cutinized cell walls along the stomatal openings. The ledges, stained dark by crystal violet, were various in form: wide with sharp edges and somewhat resembling a flying bat (BA; Figs. 1B, E, H, K, N; 2E, H; 3K), narrow and

Table 2. Examined cuticular characters and recognized character states in the Neotropical *Ocotea* complex.

Part of cuticle	Character	Character states	Abbreviation	Figures
Epidermis anticlinal walls	straightness of walls	straight to slightly curved	SC	1D, E, G, H, J, K, M, N; 2G; 3B, D
		with loose U-shaped curves	LC	2H, J, K, M, N; 3E
		with tight U-shaped curves	TC	1A, B; 2A, B, D, E; 3G, H, K, M, N
		co-occurrence of LC and TC within the same epidermis	LC-TC	3A, J
Stomata	lower stomatal ledge shape	bat-shaped	BA	1B, E, H, K, N; 2E, H; 3K
		narrow and lip-shaped	NL	2B; 3E
		butterfly-shaped	BU	2K, N; 3B, H, N
	surface appearance	circular and protruding	C	1C, F, I, L; 2F, I, L; 3I, L, O
		strongly wrinkled	SW	1O; 2O
		weakly wrinkled	WW	2C
		papillose	PA	3C
		protruding and lip-shaped or eyelid-shaped	LI	3F
	subsidiary cell evenness	uneven	UN	1N; 2B, H; 3E
		even	EV	1B, E, H, K; 2E, K, N; 3B, H, K, N

lip-shaped (NL; Figs. 2B; 3E), or wide with round edges and appearing like a butterfly (BU; Figs. 2K, N; 3B, H, N).

The surface appearance of the stomata was categorized into five types: circular and weakly to strongly protruding (C; Figs. 1C, F, I, L; 2F, I, L; 3I, L, O), strongly wrinkled (SW; Figs. 1O; 2O), weakly wrinkled (WW; Fig. 2C), papillose (PA; Fig. 3C), and lip-shaped or eyelid-shaped and protruding (LI; Fig. 3F). Circular shape varied from elliptical (e.g., Fig. 1L) to round (e.g., Fig. 3I), and circles also appeared perfect (e.g., Fig. 3O) or broken at both ends of the stomatal slit (e.g., Fig. 2L), depending on the species. The lip shape was distinguished by the protrusion of the central part of the stomatal surface, whereas the central part of other protrusions was generally depressed (compare Fig. 3F and Fig. 3I). Strongly wrinkled surfaces markedly contrasted with the other cells of the stomata or epidermis (Figs. 1O; 2O), whereas weakly wrinkled surfaces had only shallow folding around the stomata (Fig. 2C).

The subsidiary cells on each side of a stoma were more or less even, similar in size and shape (EV; Figs. 1B, E, H, K; 2E, K, N; 3B, H, K, N), or uneven and dissimilar (UN; Figs. 1N; 2B, H; 3E). The species with the even-shaped subsidiary cells, however, sometimes included stomata with slightly uneven subsidiary cells, which made the determination more difficult.

Although Christophel et al. (1996) referred the presence/absence and features of various specialized cells as a useful cuticular feature, we did not find any specialized cells for any species in this study.

Discussion

Chanderbali et al. (2001) have presented the most detailed phylogeny of the *Ocotea* complex to date, a study based on the ITS region. Such a phylogeny should be considered a theory of relationships until it can be confirmed by a different data set. This study of the cuticular features of all species included in the ITS-based phylogeny offers a test (Fig. 4). In addition, we will discuss if and to which degree cuticular features can help in the identification of specimens belonging to the *Ocotea* complex.

The first question we will address is if the cuticular characters vary within the clades recognized in Chanderbali et al. (2001). As can be seen in Figure 4, the answer is yes for some features and no for others. The character states of the anticlinal walls vary frequently within the clades. They are only constant in three clades consisting of two species each (*Endlicheria punctulata* (Mez) C. K. Allen and *Ocotea pauciflora* (Nees) Mez; *Pleurothyrium cinereum* and *P. insigne* van der Werff; the two species of *Urbanodendron*) and in the clade consisting of four species of *Licaria*.

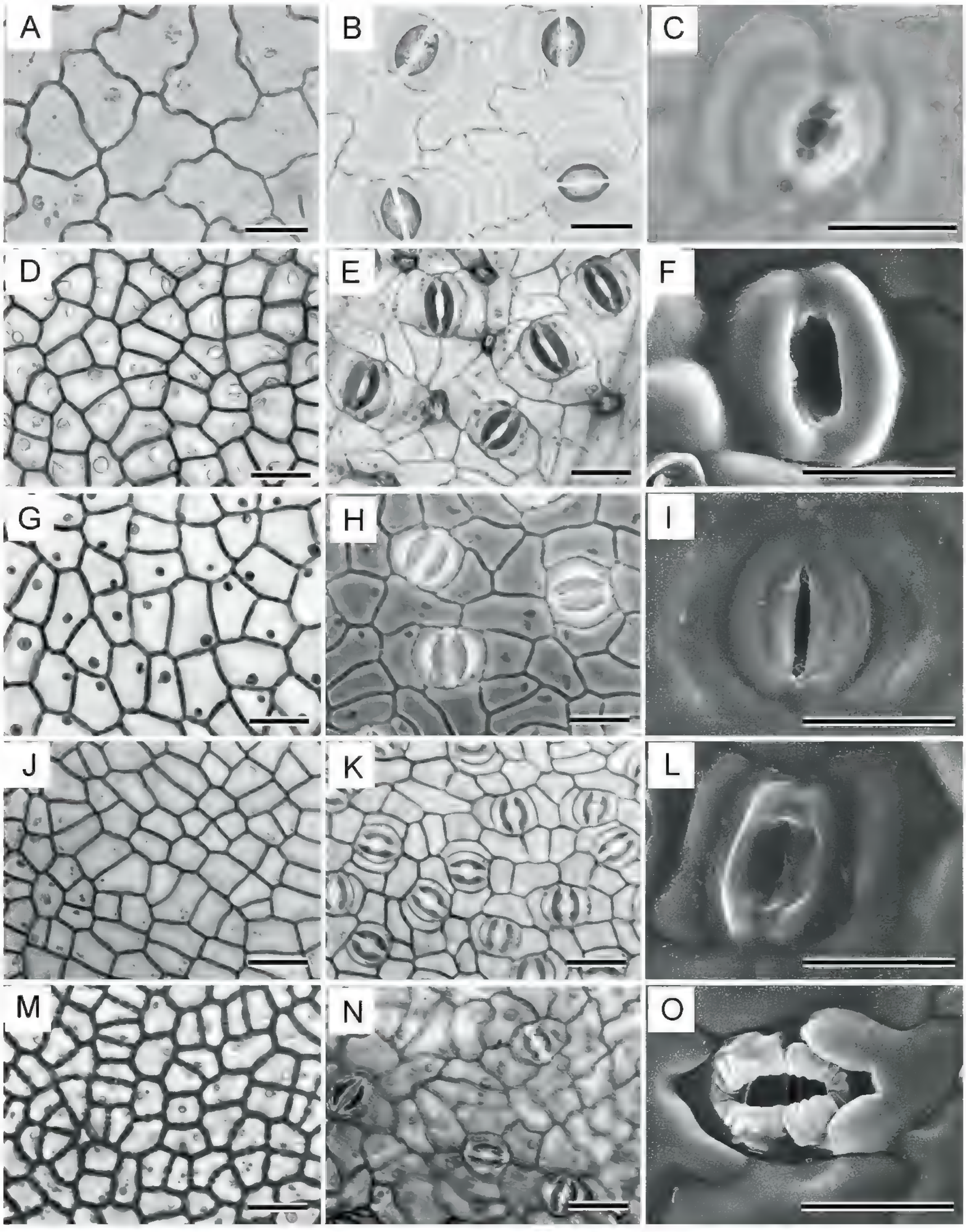

Figure 1. Optical micrographs of adaxial cuticles (A, D, G, J, M), abaxial cuticles (B, E, H, K, N), and SEMs of the stomatal complex (C, F, I, L, O). —A–C. *Endlicheria chalisea*. —D–F. *Rhodostemonodaphne praeclara*. —G–I. *Ocotea ceanothifolia*. —J–L. *Nectandra amazonum*. —M–O. *Pleurothyrium insigne*. Scale bars = 20 μm.

The character states of the subsidiary cells also show some variation within the clades, but less so than found for the anticlinal walls. This variation occurs in clade B, part of the large group of species with unisexual flowers (clades A, B, C and D), in clade L and in clade N, the four species of *Licaria*. Although clade L received strong support in the ITS-based phylogeny, its two species, *Ocotea veraguensis* (Meisn.) Mez and *O. quixos* (Lam.) Kosterm., differed both in characters of their anticlinal walls and subsidiary cells, but shared character states of the stomatal ledges and stomatal surface. We do not attach much importance to these shared stomatal character states because these two are the most common ones (out of 50 taxa 32 were scored as BA for stomatal ledges and 39 as C for stomatal surface). With one exception, the stomatal surface character states did not vary within the clades. The single exception is in clade I consisting of three species of *Aniba*; two species have a papillose surface, while the third has a strongly wrinkled surface. The papillose surface of the two species was not unexpected. In the revision of *Aniba* by Kubitzki (1982), the species were divided in three groups and one of these groups was characterized by a papillose lower leaf surface. Both *A. cinnamomiflora* and *A. panurensis* were

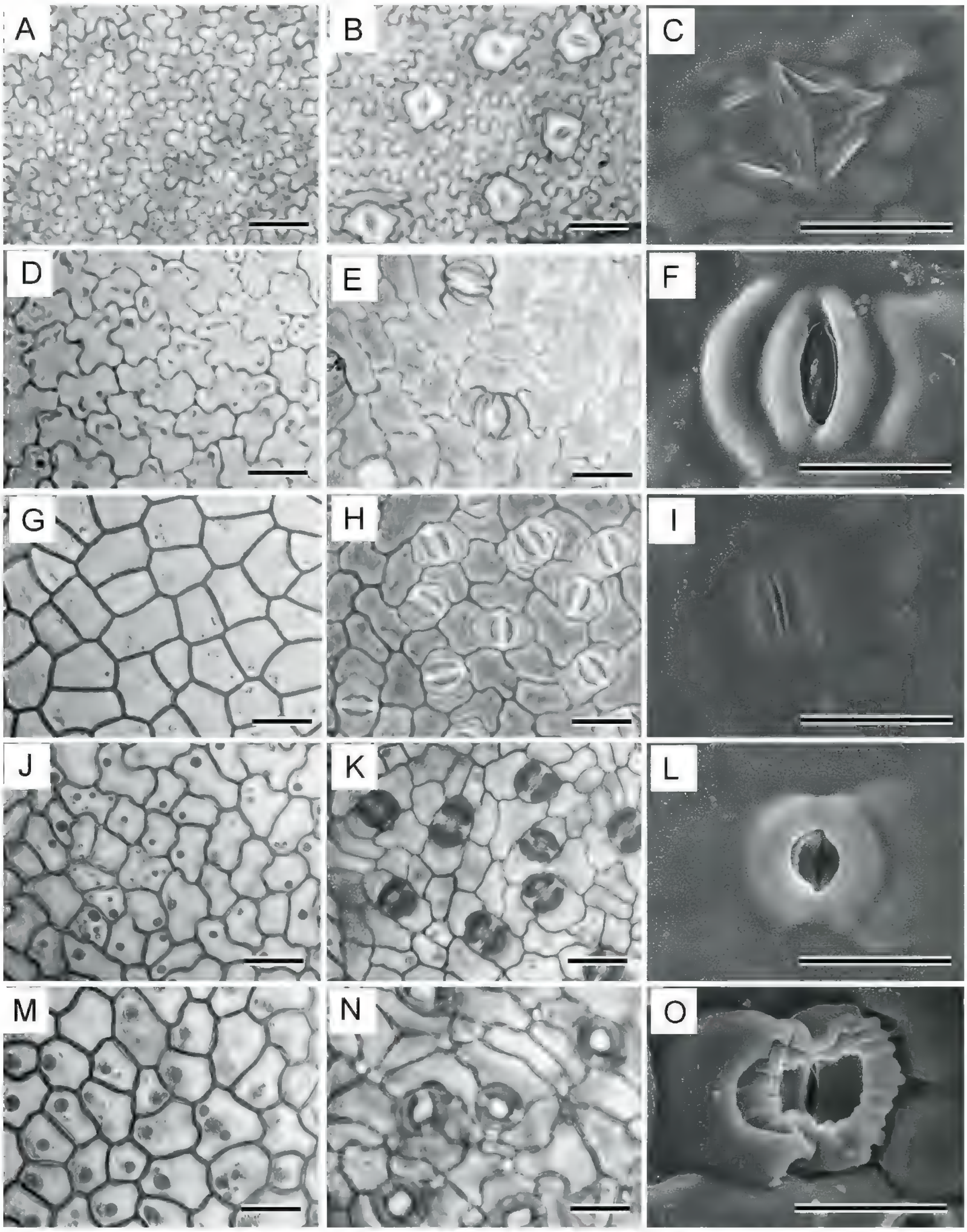

Figure 2. Optical micrographs of the adaxial cuticles (A, D, G, J, M), abaxial cuticles (B, E, H, K, N), and SEMs of the stomatal complex (C, F, I, L, O). —A–C. *Ocotea helicterifolia*. —D–F. *Umbellularia californica*. —G–I. *Nectandra purpurea*. —J–L. *Ocotea rhynchophylla*. —M–O. *Aniba excelsa*. Scale bars = 20 μm.

placed by Kubitzki (1982) in the group with a papillose lower leaf surface. Finally, the character states of the stomatal ledges did not vary at all within the clades. Thus, especially the characters of the stomatal ledges and the stomatal surface support the phylogeny of the *Ocotea* complex proposed in Chanderbali et al. (2001).

According to Christophel et al. (1996), epidermal (nonstomatal) cells have several additional characters supposedly useful for the taxonomy of the Lauraceae, including periclinal wall ornamentation, uniformity of thickness of anticlinal walls, uniformity of thickness of anticlinal walls, uniformity of cell size, and maximum cell dimension. These features are not included in Figure 4, but will be briefly discussed here. Periclinal wall ornamentation was not useful for the taxonomy of the Neotropical *Ocotea* complex, because almost all the species examined had smooth periclinal walls. Exceptions were for *Pleurothyrium cinereum* (wrinkled), *Aniba cinnamomiflora* (papillose), and *A. panurensis* (papillose), all of which broke the consistency within the clade. Uniformity of

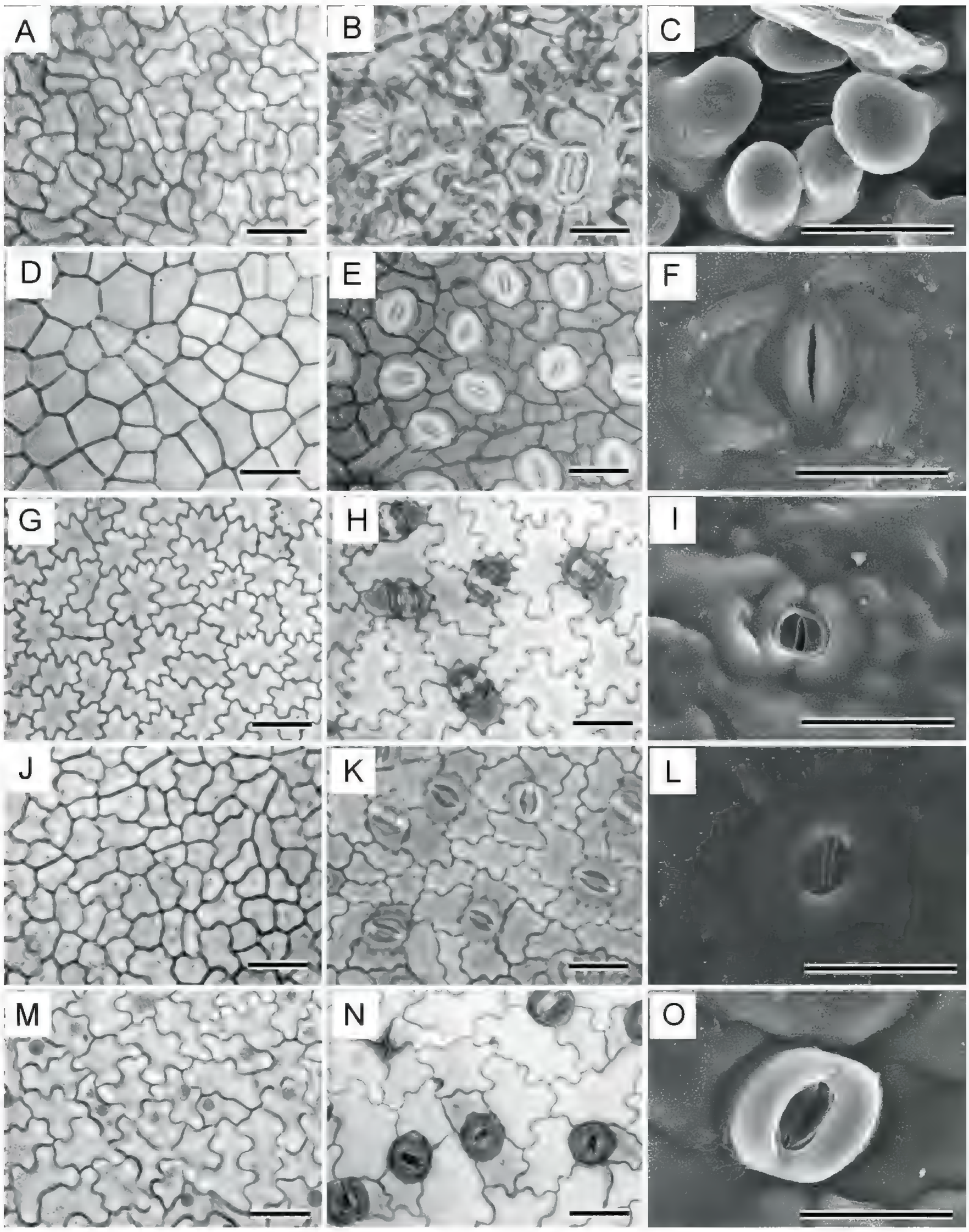

Figure 3. Optical micrographs of the adaxial cuticles (A, D, G, J, M), abaxial cuticles (B, E, H, K, N), and SEMs of the stomatal complex (C, F, I, L, O). —A–C. *Aniba panurensis*. —D–F. *Ocotea insularis*. —G–I. *Kubitzkia mezii*. —J–L. *Urbanodendron bahiense*. —M–O. *Licaria guianensis*. Scale bars = 20 μm.

thickness of anticlinal walls was not useful either, because the walls were more or less beaded and not different from each other for all the species examined. Cell size was also excluded because it is known that epidermal cell size varies according to habitat factors such as climate (Roth, 1984). Nishida and van der Werff (2007) also reported that the cell size showed so much variation within a sample that this character cannot be used to define the species.

The second question is whether any of the cuticular features are characteristic for the ITS-based clades. If we consider a single feature, the answer is no. There is no single feature characterizing a clade. This conclusion is not surprising; there are also no single floral or fruit characters allowing identification to a particular clade. The only cuticle feature indicative of a genus is the papillose surface of the stomata, which is found in two of the three *Aniba* species. Although the papillose leaf surface is rare among Lauraceae, it is not restricted to *Aniba* species; for instance, this character occurs also in *Licaria brasiliensis* (Nees) Kosterm., *L. chrysophylla* (Meisn.) Kosterm., and *L. dolichantha* Kurz (Kurz, 2000), three species not included in this study. It is

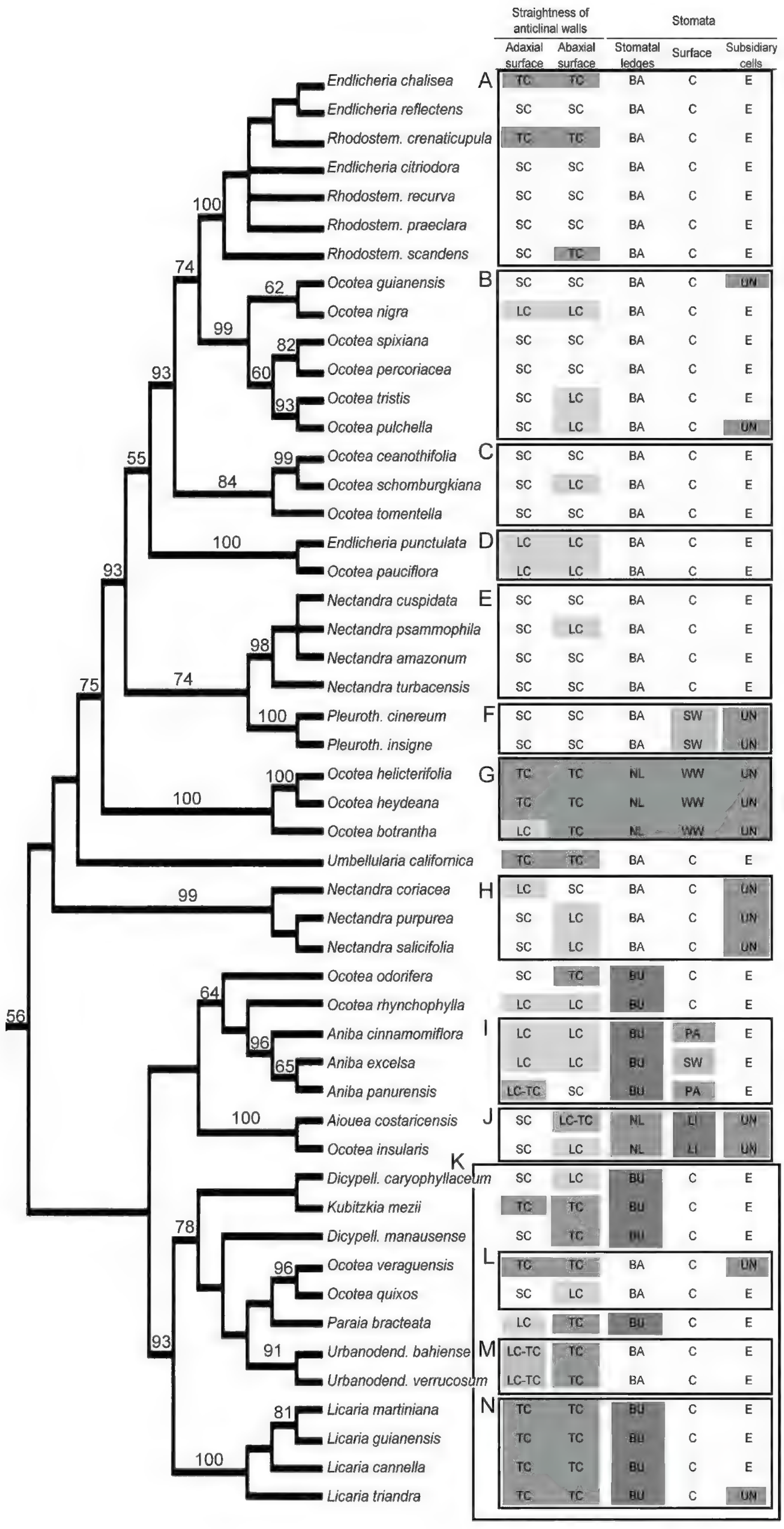

Figure 4. Comparison between the molecular phylogenetic tree (left) and cuticular character states (right). The phylogenetic tree was modified from the figure in Chanderbali et al. (2001), which was the Adams consensus of 567 equally parsimonious trees (ITS sequences) with the numbers above branches indicating bootstrap support. For convenience of comparison, cuticular features in the clades with relatively high bootstrap support by the molecular study (> 84%) were enclosed in squares as clades A–N (K includes L–N), and the same cuticular character states were colored with the same tone (cf. Table 2, Figs. 1–3). *Rhodostem.* = *Rhodostemonodaphne*, *Pleuroth.* = *Pleurothyrium*, *Dicypell.* = *Dicypellium*, *Urbanodend.* = *Urbanodendron*.

reasonable to expect that these *Licaria* species will also have papillose stomata surfaces. On the other hand, if we consider combinations of features, we find that certain clades can be defined by combinations of features, while others cannot. Examples of clades defined by cuticular features are clade F (two *Pleurothyrium* species), clade G (three central American species of *Ocotea*), and clade N (the *Licaria* species). Other clades lack a distinctive combination of features; for instance, clade E (four *Nectandra* species, with bisexual flowers) does not differ from clades A, B, C, and D (all species with unisexual flowers). Likewise, *Umbellularia californica* (Hook. & Arn.) Nutt. does not differ in cuticular features from *Endlicheria chalisea* Chanderbali or from *Rhodostemonodaphne crenaticupula* Madriñán. In general, cuticular features alone are not sufficient for assigning a specimen to a particular clade.

The third question to be addressed is if cuticular features hold promise for identifying species or characterizing genera. One could hope that cuticular features might function as a morphological bar code, allowing identification of sterile specimens without having to resort to DNA analysis. Our results indicate that this is not likely to be the case. Of the largest Neotropical genus, *Ocotea*, 10 species with unisexual flowers are included in our study. These species do not greatly differ in cuticular characters. Likewise, clade E (four species of *Nectandra*) is homogeneous and it is not possible to identify the species solely on their cuticular characters. Some genera can be identified by a particular combination of cuticular features; examples are *Pleurothyrium* (clade F), *Urbanodendron* (clade M, although one should be careful with characters of the anticlinal cell walls), and *Licaria* (clade N). The two largest genera, *Ocotea* and *Nectandra*, were found to be polyphyletic in the DNA-based analysis and it is therefore not surprising that neither of those can be defined on the basis of cuticular features.

Finally, do the cuticular features validate the DNA-based phylogeny proposed by Chanderbali et al. (2001)? The groups of species that can be recognized on the basis of cuticle characters correspond well with the clades found in the phylogenetic arrangement of the species (Fig. 4).

Of course, groupings of species have also been proposed on purely morphological grounds. In most cases there is a congruence between groups based on morphology, those based on cuticles, and those based on phylogeny. The *Ocotea helicterifolia* (Meisn.) Hemsl. group was first recognized by Rohwer (1991) and accepted by van der Werff (1999). Mez (1889) already recognized the *Ocotea* species with unisexual flowers as a distinct group (as subgenus *Oreodaphne* Nees). Van der Werff (2002) distinguished the *O. insularis* (Meisn.) Mez group (represented only by *O. insularis* in this study). *Ocotea* subg. *Dendrodaphne* (Beurl.) Mez was also already recognized by Mez (1889). Rohwer (1993) revised the species of the genus *Nectandra* and discussed the relationships of the species. He commented that the *N. coriacea* (Sw.) Griseb. group (including *N. purpurea* (Ruiz & Pav.) Mez and *N. salicifolia* (Kunth) Nees) was not linked to any other group in *Nectandra*, and he questioned whether this group really belonged to *Nectandra*. Thus, the same species groups are found in the phylogeny, in the analysis based on cuticle characters, and in species groups based on floral and fruit characters. However, there are a few cases where cuticle/phylogeny groups differ from species groups based on morphology. One example is the close relationship between *Aiouea costaricensis* (Mez) Kosterm. and *O. insularis*, first found in the phylogeny of Chanderbali et al. (2001). Renner (1982), who revised the genus *Aiouea*, regarded it as closely related to *Endlicheria* or *Aniba* and *Licaria*, but a relationship with *Ocotea* had never been proposed. This is an example of species relationships found in the phylogeny that are supported by the cuticle data but conflict with species relationships that are based on flower and fruit morphology. A second example is the group including all species with unisexual flowers (*Endlicheria*, *Rhodostemonodaphne*, and part of *Ocotea*) found in the phylogeny, which is supported by the cuticle data but is not found in relationships based on flower and fruit morphology. A third example is offered by the four species of *Licaria*. In the phylogeny and the cuticle analysis, these species form one group, but in the revision by Kurz (2000), three species groups are recognized on the basis of stamen characters. Two of these groups are represented in our study: *L. cannella* (Meisn.) Kosterm. is part of one group and the other three *Licaria* species are part of a second group. These groups based on morphology are not found in the groups based on phylogeny or on cuticle characters. Thus, in two cases, the cuticle/phylogeny groups include species from different morphology-based groups and, in the case of *Licaria*, morphology-based groups are not recognized in the cuticle/phylogeny groups.

Conclusion

Cuticles of 50 Neotropical species belonging to the *Ocotea* complex sensu Chanderbali et al. (2001) were studied. Several species groups could be recognized

on the basis of cuticle characters. These groups generally agreed with the clades found in the largest phylogenetic study to date (Chanderbali et al., 2001), and in most cases they also agreed with species groups based on floral and fruit characters. In two cases, the phylogeny and cuticles placed species belonging to different genera in the same group; these groups had not been recognized before based on flower or fruit characters. In these cases, the cuticle characters support species relationships found in the phylogeny and do not support species relationships based on flower and fruit characters. In one case, two morphology-based groups were placed in the same group based on cuticles and phylogeny. Although cuticle characters alone do not allow placement of a species in a species group or even identification of species, these characters are useful in establishing relationships between taxa and ultimately lead to a better understanding of the classification of Lauraceae.

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EL GÉNERO *GLANDULARIA* (VERBENACEAE) EN ARGENTINA[1]

Paola F. Peralta[2] *y María E. Múlgura*[2]

Resumen

Se presenta un estudio taxonómico de las especies del género *Glandularia* J. F. Gmel. que habitan en Argentina, el área de mayor diversidad del género en Sudamérica. En Argentina el género comprende 33 especies y cuatro variedades, siendo 12 taxones exclusivos de la región en estudio. Estos taxa se encuentran distribuidos desde la provincia de Jujuy al norte hasta la provincia de Santa Cruz en el sur. Se delimitan las especies en estudio y se esclarecen los problemas nomenclaturales y de tipificación. Se neotipifica: *Verbena platensis* Spreng. Se lectotipifican: *V. aristigera* S. Moore, *V. aurantiaca* Speg., *V. calliantha* Briq., *V. chamaedryfolia* Juss. f. *foliosa* Chodat, *V. flava* Gillies & Hook. ex Hook., *V. hassleriana* Briq., *V. incisa* Hook., *V. megapotamica* Spreng., *V. melindres* Gillies, *V. melindroides* Cham., *V. mendocina* Phil., *V. phlogiflora* Cham., *V. phlogiflora* var. *mucilenta* Schauer, *V. sanguinea* Larrañaga, *V. scordioides* Cham., *V. selloi* Spreng., *V. stellarioides* Cham., *V. stellarioides* var. *sessilis* Cham., *V. sulphurea* D. Don var. *pedunculata* Gay, *V. tenera* Spreng., *V. teucrioides* Gillies & Hook. ex Hook. y *V. tweedieana* Niven ex Hook. var. *arraniana* Niven en Maund & Hensl. ex Maund. Se realiza una nueva combinación a nivel subespecífico: *G. aurantiaca* (Speg.) Botta var. *glabra* (Hicken) P. Peralta, y tres a nivel específico: *G. andalgalensis* (Moldenke) P. Peralta, *G. andina* (Griseb.) P. Peralta y *G. tweedieana* (Niven ex Hook.) P. Peralta. Se incluye una clave para identificar las especies y variedades, que aquí se describen e ilustran.

Abstract

A taxonomic study of the species of the genus *Glandularia* J. F. Gmel. is presented for Argentina, with 33 species and four varieties, of which 12 taxa are exclusive to the region of study, representing the area of greatest diversity in southern South America. These taxa are distributed from the province of Jujuy in the north to the province of Santa Cruz in the south. The inclusive species are delimited in this study and nomenclatural problems and typifications are clarified. The following plant names are neotypified: *Verbena platensis* Spreng. Lectotypifications are provided for *V. aristigera* S. Moore, *V. aurantiaca* Speg., *V. calliantha* Briq., *V. chamaedryfolia* Juss. f. *foliosa* Chodat, *V. flava* Gillies & Hook. ex Hook., *V. hassleriana* Briq., *V. incisa* Hook., *V. megapotamica* Spreng., *V. melindres* Gillies, *V. melindroides* Cham., *V. mendocina* Phil., *V. phlogiflora* Cham., *V. phlogiflora* var. *mucilenta* Schauer, *V. sanguinea* Larrañaga, *V. scordioides* Cham., *V. selloi* Spreng., *V. stellarioides* Cham., *V. stellarioides* var. *sessilis* Cham., *V. sulphurea* D. Don var. *pedunculata* Gay, *V. tenera* Spreng., *V. teucrioides* Gillies & Hook. ex Hook., *V. tweedieana* Niven ex Hook. var. *arraniana* Niven in Maund & Hensl. ex Maund. One new combination at subspecific level is made: *G. aurantiaca* (Speg.) Botta var. *glabra* (Hicken) P. Peralta, and three at specific level: *G. andalgalensis* (Moldenke) P. Peralta, *G. andina* (Griseb.) P. Peralta, and *G. tweedieana* (Niven ex Hook.) P. Peralta. Included is a key to identify the species and varieties in Argentine *Glandularia*, which are described and illustrated.

Key words: Argentina, *Glandularia*, Verbenaceae.

La familia Verbenaceae está ampliamente representada en las regiones templadas, tropicales y subtropicales de América del Norte, Central y del Sur, África e India. El centro de mayor diversidad de la familia se encuentra en las regiones subtropicales y subáridas de Sudamérica, desde la cordillera Mexicana central a los Andes centrales (Sanders, 2001). La familia Verbenaceae s. str. (Junell, 1934; Cantino, 1992; Judd et al., 1999; Atkins, 2004) comprende 34 géneros y ca. 1200 especies (Atkins, 2004). En Argentina está representada por 26 géneros y alrededor de 240 especies, siendo 54 endémicas.

Glandularia J. F. Gmel. es un género exclusivamente americano, de distribución disyunta. Comprende alrededor de 100 especies (Atkins, 2004), distribuidas desde Estados Unidos de América hasta Guatemala en el hemisferio norte, mientras que en el

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hemisferio sur, se encuentra en la Argentina, Bolivia, Brasil, Chile, Paraguay, Perú y Uruguay. En la Argentina hay una gran diversidad específica, las que se distribuyen en forma continua desde Jujuy al norte hasta la provincia de Santa Cruz, en el sur aproximadamente entre los 56°5′ y los 72° de longitud oeste y desde los 22° y los 51° de latitud sur. Las especies crecen desde el nivel del mar, a lo largo de toda la costa Argentina hasta los 4600 m, en la provincia fitogeográfica Altoandina en la provincia de Jujuy, según el criterio de Cabrera y Willink (1973). Las especies habitan en lugares abiertos como campos graminosos o praderas, bordes de caminos, laderas de cerros, margen de selvas o bosques.

Linnaeus funda en 1753 el género *Verbena*. En 1791 Gmelin describe al género *Glandularia*, sobre la base de *Anonymus carolinensis* T. Walter, hoy *G. carolinensis* J. F. Gmel. sinónimo de *G. canadensis* (L.) Nutt. Sin embargo diferentes autores consideraron a *Glandularia* como una sección (Walpers, 1845; Schauer, 1847; Briquet, 1895; Reiche, 1910; Perry, 1933) o como un subgénero del género *Verbena* (Bentham & Hooker, 1876; Lewis & Oliver, 1961), por su parte Moldenke, entre 1940 y 1983, tampoco aceptó a *Glandularia* como género independiente de *Verbena* (Moldenke, 1940, 1941, 1942a, 1942b, 1946, 1947, 1948a, 1948b, 1949a, 1949b, 1950, 1953, 1955, 1956, 1958, 1961a, 1961b, 1962, 1963a, 1963b, 1964a, 1964b, 1964c, 1964d, 1964e, 1968, 1969, 1972, 1975, 1979, 1981, 1983; Moldenke & Moldenke, 1949).

Autores que tratan a *Glandularia* como género son Small en 1933, donde describe las especies que crecen al suroeste de Estados Unidos y Schnack y Covas (1944) y Schnack (1964), quienes dan a conocer por primera vez los argumentos por los cuales *Glandularia* debe tratarse como género independiente considerando: número básico de cromosomas, ploidía, tamaño de los cromosomas, anatomía del tallo, apéndices glandulares conectivales, longitud del estilo en relación con el ovario, desarrollo del conectivo en relación con las tecas. Luego este criterio fue seguido por Troncoso (1974), Umber (1979), Botta y Poggio (1988), Botta (1989, 1990, 1992, 1993), O'Leary et al. (2007) y O'Leary y Peralta (2007).

Respecto al tratamiento infragenérico del género *Glandularia*, Troncoso (1974) establece las secciones *Glandularia* y *Nobiles* (Schauer) Tronc., basándose en la morfología floral. En 1978, Schnack y Covas agrupan las especies en dos subgéneros teniendo en cuenta el hábito general y caracteres de los frutos: *Glandularia* y *Paraglandularia* Schnack & Covas.

Posteriormente Umber (1979), revalua las secciones creadas por Troncoso (1974) y pasa a la sinonimia de la sección *Glandularia* la sección *Nobiles* y establece, tomando en consideración características del fruto, la sección *Rupes* Umber. Botta en 1989 retoma el criterio de Schnack y Covas (1978) y recientemente Sanders (2001), vuelve a validar la clasificación infragenérica con dos secciones previamente establecida por Troncoso (1974). En la presente contribución no se considera la clasificación infragenérica, por no realizarse en esta oportunidad el estudio general del género.

Materiales y Métodos

Se han seguido los métodos clásicos para este tipo de estudio, analizando ejemplares de herbario y en algunos casos plantas vivas, consultándose las descripciones originales, ejemplares tipo y material de herbario de cada uno de los taxones. Los herbarios consultados, citados conforme a las siglas que figuran en Holmgren et al. (1990), fueron los siguientes: B, BAB, BAF, BM, BR, CAS, CONC, CORD, CTES, F, G, G-DC, G-BOIS, G-BU, HBR, ICN, K, LIL, LL, LP, MA, MBM, MO, MPUC, NY, P, PACA, S, SGO, SI, SP, TEX, UC, UPCB, US y W. En el Apéndice 1 se brinda la lista completa de nombres científicos, incluyendo los sinonimos, en el Apéndice 2 se da la lista de los nuevos sinonimos y en el Apéndice 3 se da la lista completa de colectores de los ejemplares estudiados.

Caracteres Morfológicos

hábito

Las formas biológicas que se observan en *Glandularia*, basadas en la terminología de Cabrera (1957), se reúnen principalmente en dos grupos: Hemicriptófitos, dentro de los cuales pueden encontrarse las siguientes variantes. *Hemicriptófitos rastreros* en donde las ramas vegetativas pueden desarrollar raíces adventicias en los nudos, las ramas floríferas son ascendentes como en *G. peruviana* (L.) Small, *G. pulchella* (Sweet) Tronc., *G. tenera* (Spreng.) Cabrera y *G. tomophylla* (Briq.) P. Peralta. *Hemicriptófitos erectos*, apoyantes o no, como *G. sessilis* (Cham.) Tronc., *G. stellarioides* (Cham.) Schnack & Covas y *G. tristachya* (Tronc. & Burkart) Schnack & Covas. El otro grupo representa los caméfitos del tipo *sufrútice* como *G. hassleriana* (Briq.) Tronc. y *G. megapotamica* (Spreng.) Cabrera & G. Dawson; algunas especies pueden formar grandes matas lignificadas en la base con ramas de renuevo anuales en la periferia como en *G. araucana* (Phil.) Botta, o

formar sufrútices enanos como en *G. microphylla* (Kunth) Cabrera.

El ciclo de vida de todas las especies del género *Glandularia* es perenne; aunque en la descripción principal de *G. nana* (Moldenke) Tronc., *G. mendocina* (Phil.) Covas & Schnack y *G. dissecta* (Willd. ex Spreng.) Schnack & Covas, Moldenke (1949a), Philippi (1870) y Sprengel (1825), respectivamente, mencionan esto que dichas especies poseen un ciclo anual, es incorrecto, ya que el hábito se ha podido corroborar con el cultivo de las mismas.

INDUMENTO

Los tricomas observados son de dos tipos: glandulares y no glandulares. Los tricomas glandulares presentan un pie formado por una sola célula, la cual puede presentarse con diferentes longitudes dando origen a tricomas glandulares cortos o largos, una cabezuela unicelular y base multicelular. Es común encontrar glándulas pateliformes en las hojas, brácteas y cálices, como en *Glandularia aristigera* (S. Moore) Tronc., *G. cheitmaniana* (Moldenke) Botta & Poggio, *G. megapotamica*, *G. mendocina*, *G. subincana* Tronc. y *G. tenera*. Los tricomas no glandulares son unicelulares, terminan en un extremo agudo y pueden ser de diferente longitud.

El tipo de pubescencia: hirsuta, híspida, estrigosa, pubérula y la distribución de los tricomas glandulares y no glandulares son caracteres constantes a nivel específico, siendo variable la densidad de los mismos intraespecifícamente.

HOJAS

Las hojas son opuestas y la venación es pinnada; cuando la lámina presenta división puede ser pinnatilobada, pinnatipartida o pinnatisecta. La morfología foliar es muy variable en cuanto al desarrollo del pecíolo, incisión de la lámina, lóbulos y margen. El pecíolo puede estar ausente como en *Glandularia sessilis* y *G. stellarioides*, brevemente desarrollado, por ejemplo en *G. incisa* (Hook.) Tronc. y *G. venturii* (Moldenke) Botta, o puede estar claramente desarrollado, pudiendo éste diferenciarse notablemente de la lámina, *G. phlogiflora* (Cham.) Schnack & Covas y *G. scrobiculata* (Griseb.) Tronc., o presentar la misma morfología, como ocurre en las hojas de las especies con lámina muy dividida (en este caso se considera el pecíolo desde la inserción al eje hasta el primer par de lóbulos, como en *G. andina* (Griseb.) P. Peralta, *G. aristigera*, *G. cabrerae* (Moldenke) Botta, *G. cheitmaniana*, *G. subincana* y *G. tenera*). La lámina puede ser entera, de contorno ovado, angostamente ovado, linear, con margen crenado, dentado, lacerado, serrado en *G. incisa*, *G. megapotamica*, *G. nana*, *G. platensis* (Spreng.) Schnack & Covas, *G. tristachya* o dividida en donde se distinguen tres grandes grupos con sus variantes:

(1) Lámina lobada: dividida en gajos o lobos no demasiado profundos, 3-lobada o 5-lobada como en *Glandularia aurantiaca* (Speg.) Botta.
(2) Lámina partida: la insición llega hasta la mitad de la lámina entre el lóbulo de la lámina y el nervio medio sin llegar a él, varían de 3-partidas a 5-partidas. Las láminas pueden ser bipinnatipartidas o tripinnatipartidas, como en *Glandularia microphylla*.
(3) Lámina secta: la insición llega hasta la vena media, pudiendo ser 3-sectas o 5-sectas. Siendo también bipinnatisectas a tripinnatisectas como en *Glandularia aristigera*, *G. parodii* Covas & Schnack, *G. subincana* y *G. tenera*.

También pueden encontrarse en un mismo individuo hojas enteras y hojas divididas, como es el caso de *Glandularia araucana* y *G. flava* (Gillies & Hook. ex Hook.) Schnack & Covas.

Cuando la lámina presenta divisiones el contorno puede ser triangular, ovado a anchamente ovado, obovado a anchamente obovado. El ápice generalmente es agudo y la base puede ser truncada como en *Glandularia tweedieana* (Niven ex Hook.) P. Peralta, decurrente en *G. stellarioides* o atenuada en *G. cabrerae*.

Debido a la presencia de yemas múltiples se desarrollan, como ocurre en otros géneros de la familia, braquiblastos menores con fascículos de hojas con las mismas características que las hojas del macroblasto, pero sin flores.

INFLORESCENCIAS

Las inflorescencias se presentan en monobotrios o pleiobotrios heterotéticos a veces paniculiformes, o con 1 ó 2 pares de paracladios generalmente frondosos y que superan la florescencia principal. Las florescencias se presentan en espigas densas, multifloras, umbeliformes en la antesis con el raquis alargado o no en la fructificación (Martínez et al., 1996).

BRÁCTEAS

Son siempre enteras, de margen entero, generalmente ciliado y con la misma pubescencia que el cáliz; en ocasiones son glabras. El tamaño varía en

relación al cáliz pudiendo ser mayores, iguales o menores a la mitad de la longitud de éste.

FLORES

Las flores son perfectas, levemente zigomorfas, con pedicelo muy breve. El cáliz es tubular, 5-dentado, con dientes subiguales, en general los abaxiales más desarrollados que los adaxiales. El cáliz fructífero persistente es más largo que las clusas y se presenta generalmente plegado y contorto a la madurez; la dehiscencia se produce por una línea longitudinal. La corola es hipocraterimorfa, conspicua, blanca, blanco-crema, amarilla, rosa, lila a roja. Puede existir una graduación en el color dentro de una misma especie e incluso dentro de la misma planta. El limbo es extendido, 5-lobado, con lóbulos subiguales, generalmente emarginados, a veces recurvos; el tubo corolino está bien desarrollado, exteriormente puede ser glabro (*Glandularia aurantiaca*, *G. peruviana*, *G. radicata* (Moldenke) Tronc. ex Múlgura, *G. sulphurea* (D. Don) Schnack & Covas), pubescente (*G. andina*, *G. scrobiculata* (Griseb.) Tronc., *G. selloi* (Spreng.) Tronc.), o en algunos casos glanduloso (*G. phlogiflora*, *G. platensis*); interiormente presenta una banda longitudinal y abaxial de tricomas agudos, adpresos y retrorsos.

ANDROCEO

El androceo está formado por cuatro estambres didínamos, insertos en la mitad superior del tubo corolino, con filamentos breves a veces el par abaxial exerto, anteras ovales, basifijas; pueden presentar apéndices conectivales en el dorso, los cuales se clasifican en:

(1) Apéndices con pie y cabeza claramente desarrollado: el pie puede tener distinta longitud. Los apéndices en general sobrepasan la longitud de las tecas y pueden sobresalir por la garganta corolar (*Glandularia selloi*, *G. sulphurea*, *G. tenera*). Figura 1C.
(2) Apéndices reducidos: presentan un pie y una cabeza, pero son de menor longitud que los anteriores, no sobrepasan la longitud de las tecas ni sobresalen por la garganta corolar (*Glandularia aurantiaca*, *G. cabrerae*, *G. macrosperma*). Figura 1B.
(3) Apéndices sin pie: en estos casos sólo está desarrollada la cabeza del apéndice, la cual se posa sobre el tejido conectivo, nunca sobrepasan las tecas ni la garganta corolar (*Glandularia guaranitica* Tronc., *G. phlogiflora*, *G. megapotamica*). Figura 1A.

GINECEO

El gineceo presenta el estilo filiforme, más de tres veces el largo del ovario, estigma bilobado, lóbulo anterior estigmatífero, a veces apenas exerto, base no ensanchada o apenas ensanchada. Ovario bicarpelar, bilocular, con un óvulo por lóculo.

Número básico de cromosomas. $x = 5$ (Botta, 1989).

Fruto. El fruto es seco y dividido en cuatro clusas subcilíndricas de sección subtrígona, de ápice obtuso o redondeado como en *Glandularia platensis*, *G. tomophylla* y *G. stellarioides*, o más o menos apiculado o rostrado como en *G. flava*, *G. lilloana* (Moldenke) Botta y *G. tenera*. La base de las clusas es angostada y sin dicho repliegue como en *G. parodii*, *G. andina* y *G. sessilis*.

FENOLOGÍA

Las especies de *Glandularia*, y en general del resto de las Verbenaceae, poseen una floración prolongada, desde mediados de octubre hasta mediados de abril, para el hemisferio sur, aunque muchos ejemplares que crecen en zonas templado-cálidas, la floración puede comenzar desde el principio de la primavera y prolongarse hasta comenzado el invierno. Pueden observarse flores y frutos en un mismo ejemplar y en la misma florescencia, hacia el ápice las flores y hacia la base los frutos.

TRATAMIENTO TAXONÓMICO

Glandularia se ubica, dentro de la familia Verbenaceae, en la tribu *Verbeneae* Schauer (Troncoso, 1974). Esta tribu ha sido redefinida por Atkins (2004: 460), autora que la caracteriza por poseer fruto seco esquizocárpico, separado a la madurez en cuatro clusas; anteras con tecas paralelas, o apenas divergentes, a menudo con conectivo dilatado; estilo 2-lobado, lóbulo anterior estigmatífero.

CLAVE PARA RECONOCER LOS GÉNEROS DE LA TRIBU VERBENEAE

1a. Estambres fértiles 2; cáliz acrescente en el fruto ..... *Hierobotana* Briq.
1b. Estambres fértiles 4; cáliz no acrescente en el fruto.
  2a. Subarbustos o plantas en cojín; inflorescencias generalmente no ramificadas (a veces con ramificación simple); clusas con base angostada; cromosomas $x = 9$ o $x = 10$.
    3a. Conectivo de las anteras no sobrepasando las tecas ..... *Junellia* Moldenke
    3b. Conectivo de las anteras sobrepasando las tecas ..... *Mulguraea* N. O'Leary & P. Peralta

2b. Hierbas anuales o perennes, no angostada; inflorescencias ramificadas (a veces condensadas con apariencia de inflorescencia simple); clusas con base engrosada; cromosomas $x = 5$ o $x = 7$.
4a. Espigas cilíndricas laxas o densas, no contraídas en la floración; estilo generalmente no más de 3 veces la longitud del ovario; cáliz maduro más corto que el fruto y con dientes no contortos; cromosomas $x = 7$ ..... *Verbena* L.
4b. Espigas generalmente contraídas en la floración; estilo generalmente más de 3 veces la longitud del ovario; cáliz maduro usualmente más lardo que el fruto y con dientes contortos; cromosomas $x = 5$ ..... *Glandularia* J. F. Gmel.

Glandularia J. F. Gmel., Syst. Nat., ed. 13 [bis] 2(2): 886, 920. 1791 [1792]. *Verbena* L. subg. *Glandularia* (J. M. Gmel.) Nutt., J. Acad. Nat. Sci. Philadelphia 2(1): 123. 1821. *Verbena* sect. *Glandularia* (J. F. Gmel.) Schauer, Prodr. [DC.] 11: 550. 1847. TIPO: *Glandularia carolinensis* J. F. Gmel. [= *Glandularia canadensis* (L.) Nutt., based on *Buchnera canadensis* L.].

Shuttleworthia Meisn., Pl. Vasc. Gen. [Meisner] 1: 290. 1840, nom. inval.

Uwarowia Bunge, Bull. Sci. Acad. Imp. Sci. Saint-Pétersbourg 7: 278. 1840. TIPO: *Uwarowia chrysanthemifolia* Bunge.

Verbena sect. *Verbenaca*, B *Foliosae*, II *Macrantae* Walpers p.p., Repert. Bot. Syst. 4: 26–32. 1845, nom. inval.

Verbena sect. *Verbenaca*, ser. *Nobilis* Schauer, Prodr. [DC.] 11: 537. 1847. TIPO: *Verbena chamaedryfolia* Juss., nom. illeg. [= *Glandularia peruviana* (L.) Small].

Verbena subg. *Glandularia* (J. F. Gmel.) W. H. Lewis & R. L. Oliv., Amer. J. Bot. 48: 638–642. 1961, nom illeg., non *Verbena* subg. *Glandularia* (J. F. Gmel.) Nutt., J. Acad. Nat. Sci. Philadelphia 2(1): 123. 1821. TIPO: *Verbenella chamaedryfolia* (Juss.) Spach [= *Glandularia peruviana* (L.) Small].

Hierbas o sufrútices rastreros, radicantes en la base o postrado-ascendentes, menos comúnmente erectos desde la base; tallos cilíndricos o subtetrágonos, macizos o fistulosos, a veces leñosos desde la base. Hojas opuestas, sésiles o pecioladas; lámina entera o dividida, desde 3- ó 5-lobadas, 3- ó 5-partidas a 3- ó 5-sectas, bipinnatipartidas o 2- ó 3-pinnatisectas, glabras o pubescentes con indumento variado, tricomas simples y/o glandulares. Inflorescencia en pleiobotrio heterotético o monobotrio; florescencias son espigas multifloras, densas, generalmente alargadas a la madurez de los frutos. Flores hermafroditas, gamosépalas, gamopétalas, levemente zigomorfas, brevemente pediceladas; cáliz pubescente, tubuloso, 5-costado, 5-dentado, dientes subiguales, triangulares, filiformes, subulados; corola hipocraterimorfa, conspicua, exteriormente glabra o pubescente, tubo recto o ligeramente encorvado, limbo extendido, 5-lobado, lóbulos bilobados, emarginados, blanca, amarilla, lila, rosa, interior del tubo corolino siempre pubescente, fauce pubescente o no; estambres 4, didínamos, insertos en la mitad superior del tubo corolino, conectivo no sobrepasando la longitud de las tecas, generalmente con apéndices conectivales, que sobrepasan la garganta corolar o no, filamentos breves, anteras ovales, basifijas; ovario 2-carpelar, 2-locular, con 1 óvulo por lóculo; estilo filiforme más de tres veces la longitud del ovario, estigma bilobado, lóbulo abaxial estigmatífero. Fruto esquizocárpico, seco, dividiéndose a la madurez en 4 clusas cilíndricas de ápice rostrado o no, pericarpio extendido o no; cáliz fructífero persistente, plegado y contorto en el ápice, hendido lateralmente. Número básico de cromosomas: $x = 5$ (Botta, 1989).

Clave de las Especies y Variedades de *Glandularia*

1a. Plantas con la lámina foliar generalmente entera (a excepción de *G. flava*) linear, ovada a oblonga, con margen liso, crenado, serrado o lobado; fauce da la corola pubescente; par superior de estambres con o sin apéndices conectivales.
2a. Espigas contraídas, raquis no alargado en la fructificación; par superior de estambres con apéndices conectivales sin pie; clusas con ápice brevemente rostrado.
3a. Tallos, hojas y cáliz ralamente estrigosos..... 14. *G. megapotamica*
3b. Tallos, hojas y cáliz híspido-glandulosos, hirsutos, hirsuto-escabrosos.
4a. Tallos hirsuto-escabrosos; brácteas angostamente ovadas a subuladas, de 5–6 mm long., pestañosas y escasamente hirsutas; cáliz híspido-glanduloso sobre las costillas, resto glabro; dientes del cáliz subulados..... 20. *G. phlogiflora*
4b. Tallos híspido-glandulosos; brácteas basales de 1.5–2 mm long., ovales; superiores de 2–3 mm long., ovales a angostamente ovadas, pubescencia híspida a estrigosa; cáliz densamente híspido-estrigoso con algunos tricomas glandulares; dientes del cáliz triangulares..... 10. *G. guaranitica*
2b. Espigas alargadas, raquis alargado en la fructificación; par superior de estambres con o sin apéndices conectivales; clusas con ápice redondeado o rostrado.
5a. Brácteas iguales o menores a la mitad de la longitud del cáliz.

6a. Plantas generalmente glabras, hojas a veces irregularmente partidas; corolas amarillas; par superior de estambres con apéndices conectivales exertos; clusas con ápice rostrado..... 9. *G. flava*
6b. Plantas de pubescencia variada y glandulosa, hojas siempre enteras; corolas blancas, en tonos de rojo o en tono de lila; par superior de estambres sin apéndices conectivales; clusas con ápice obtuso o no.
7a. Clusas mayores de 5.5 mm long., con ápice rostrado ..... 17. *G. nana*
7b. Clusas menores de 5 mm long., con ápice obtuso.
8a. Pubescencia marcadamente glandular en toda la planta; hojas angostamente ovadas a lineares, con margen crenado hasta lobado; flores blancas..... 21. *G. platensis*
8b. Pubescencia glandular escasa en toda la planta; hojas triangulares-oblongas, ovadas a elípticas, con margen dentado, serrado o inciso-lobado; flores rojas o rosadas.
9a. Hojas dimorfas: inferiores triangular-oblongas, inciso-lobadas, truncadas o subcordadas; superiores angostamente ovadas, inciso-serradas; pubescencia cano-hirsuta ..... 32. *G. tweedieana*
9b. Hojas homomorfas: ovadas a elípticas, base generalmente cuneada, margen regular o irregularmente crenado o serrado; pubescencia híspida..... 19. *G. peruviana*
5b. Brácteas mayores a la mitad de la longitud del cáliz.
10a. Hojas pecioladas, lámina elíptico-ovada u ovado-triangular, estrigosa, margen marcadamente serrado, crenado hasta profundamente lobado.
11a. Brácteas 9–10.5 mm de long., lámina elíptico-ovada; par superior de estambres sin apéndices conectivales; clusas rostradas ..... 11. *G. hassleriana*
11b. Brácteas 3.5–6 mm de long., lámina ovado-triangular; par superior de estambres con apéndices conectivales; clusas redondeadas..... 23. *G. scrobiculata*
10b. Hojas sésiles, lámina linear a angostamente ovada, generalmente glabra o escasamente estrigosa, margen liso o levemente serrado.
12a. Hoja con base atenuada; brácteas 4–4.5 mm long.; dientes del cáliz de 0.5 mm long.; par superior de estambres sin apéndices conectivales; clusas 4–4.5 mm long... 31. *G. tristachya*
12b. Hoja con base cordada o decurrente; brácteas mayores de 6 mm long.; dientes del cáliz mayores de 1 mm long.; par superior de estambres con apéndices conectivales; brácteas mayores de 6 mm long.; dientes del cáliz mayores de 1 mm long.; clusas menores de 4 mm long.
13a. Hojas con base decurrente; brácteas mayores que el cáliz (10–14 mm long.)..... 26. *G. stellarioides*
13b. Hojas con base truncada a veces cordada; brácteas iguales a la longitud del cáliz, o apenas menores (6–8 mm long.)..... 25. *G. sessilis*
1b. Plantas con lámina foliar 3-lobada, 3-partida, 5-partidas, 3-sectas a 5-sectas, margen de los lóbulos enteros a veces dentados o lobulados; par superior de estambres con apéndices conectivales.
14a. Brácteas iguales o mayores a la mitad de la longitud del cáliz.
15a. Par superior de estambres con apéndices conectivales menores a la longitud de las tecas, inclusos en la garganta corolar.
16a. Superficie foliar glabra o con escasos tricomas cortos y rígidos, consistencia subcrasas, lóbulos elípticos a espatulados, ápice redondeado; corolas amarillas pálidas a rosadas..... 5. *G. aurantiaca*
16b. Superficie foliar estrigosa o estrigosa-glandular, consistencia nunca subcrasa; lóbulos lineares o angostamente ovados, ápice agudo; corolas violetas, lilas, azules.
17a. Ramas y cáliz híspidos-glandulosos, hojas estrigosas-glandulares ..... 33. *G. venturii*
17b. Ramas, cáliz y hojas estrigosas o híspidas, sin tricomas glandulares.
18a. Brácteas anchamente ovadas, 5–6.5 mm long.; clusas curvadas ..... 12. *G. lilloana*
18b. Brácteas ovadas a angostamente ovadas, menores de 5 mm long.; clusas rectas.
19a. Hojas con pecíolo mayor de 3 mm long.; dientes del cáliz caudados; corola escasamente pubescente en el exterior; clusas menores de 2.5 mm long..... 7. *G. cheitmaniana*
19b. Hojas con pecíolo 2–3 mm long.; dientes del cáliz subulados; corola glabra en el exterior; clusas 3–4 mm long..... 6. *G. cabrerae*
15b. Par superior de estambres con apéndices conectivales de mayor longitud que las tecas, generalmente exertos.
20a. Hemicriptófitos erectos; corola externamente glabra.
21a. Hojas sésiles o con pecíolo hasta de 5 mm long., de contorno oval-triangular; cáliz con pubescencia cano-hispídula, dientes del cáliz subulados; clusas de 2.5–2.8 mm long ..... 27. *G. subincana*
21b. Hojas con pecíolo de 5–8 mm long., contorno ovado; cáliz con pubescencia híspida, dientes del cáliz aristados; clusas 3–3.5 mm long..... 15. *G. mendocina*
20b. Hemicriptófitos rastreros; corola con pubescencia externamente variable.
22a. Cáliz con pubescencia generalmente estrigosa; apéndices conectivales generalmente no sobresaliendo de la garganta corolar; clusas menores de 3 mm long.
23a. Lámina foliar 2/3 superior lobada y 1/3 basal sectada, lóbulos lobados; superficie abaxial híspida..... 30. *G. tomophylla*
23b. Lámina foliar 5-sectada, lóbulos partidos o sectados; ambas superficies estrigosas ..... 2. *G. andina*

22b. Cáliz con pubescencia híspida; apéndices conectivales generalmente sobresaliendo de la garganta corolar; clusas mayores de 3 mm long.
24a. Lámina foliar con lóbulos angostamente ovados, superficie adaxial glabra o escasamente estrigosa; clusas con ápice redondeado ..... 24. *G. selloi*
24b. Lámina foliar con lóbulos filiformes, superficie adaxial híspida a adpresa; clusas con ápice apiculado ..... 18. *G. parodii*
14b. Brácteas menores a la mitad de la longitud del cáliz.
25a. Ramas adultas glabras o glabrescentes (escasamente estrigosas).
26a. Ramas escasamente estrigosas; hojas y brácteas estrigosas.
27a. Dientes del cáliz tubulados; apéndices conectivales generalmente sobresaliendo de la garganta corolar; clusas apiculadas ..... 29. *G. tenera*
27b. Dientes del cáliz filiformes; apéndices conectivales no sobresaliendo de la garganta corolar, no superando la longitud de las tecas; clusas con ápice redondeado..... 4. *G. aristigera*
26b. Ramas glabras o cuando jóvenes pubérulas; hojas generalmente glabras o escasamente estrigosas; cáliz glabro o hispídulo sólo en la base.
28a. Sufrútice; hojas no carnosas, 3-lobadas, 3- ó 5-partidas a bipinnatípartidas; corolas amarillas, crema o blancas.
29a. Sufrútice erecto; hojas angostamente ovadas, pecíolo de 5–7 mm long.; clusas con ápice obtuso..... 3. *G. araucana*
29b. Sufrútice postrado; hojas linear a ovado-elípticas, sésiles; clusas con ápice rostrado ..... 9. *G. flava*
28b. Hemicriptófito rastrero; hojas subcarnosas triangular, 3- ó 5-sectas, bipinnatipartidas; corola lila o violeta..... 22. *G. radicata*
25b. Ramas maduras híspidas.
30a. Raquis de la florescencia no alargado en la fructificación; brácteas lineares a angostamente ovadas; clusas de 2–2.5 mm long..... 8. *G. dissecta*
30b. Raquis de la florescencia alargado en la fructificación; brácteas triangulares, ovadas o angostamente ovadas; clusas mayores de 2.5 mm long.
31a. Par superior de estambres con apéndices conectivales reducidos, no superando la longitud de las tecas; clusas 5–6 mm long ..... 13. *G. macrosperma*
31b. Par superior de estambres con apéndices conectivales superando la longitud de las tecas; clusas menores de 4 mm long.
32a. Hemicriptófito rastrero; brácteas triangulares de 1.5–2 mm long.; clusas apiculadas ..... 1. *G. andalgalensis*
32b. Sufrútices; brácteas ovadas a angostamente ovadas; clusas con ápice obtuso.
33a. Sufrútice enano (5–10 cm); cáliz y brácteas híspidas a estrigosas; corola pubescente, lila o blanca ..... 16. *G. microphylla*
33b. Sufrútice ascendente (20–25 cm altura); cáliz y brácteas híspido-glandulares; corola glabra, amarilla ..... 28. *G. sulphurea*

1. Glandularia andalgalensis (Moldenke) P. Peralta, comb. nov. Basiónimo: *Verbena andalgalensis* Moldenke, Phytologia 5: 227. 1955. TIPO: Argentina. Catamarca: Andalgalá, Pampa del Arenal, 2700 m, mar. 1916, *P. Jörgensen 1613* (holotipo, UC no visto; isotipos, LL no visto, LL foto SI!, SI 3671!, SI 3672!, UC foto SI!; US 11866!, US foto SI!). Figura 2.

Hemicriptófito rastrero, muy ramificado; ramas híspidas; entrenudos de 0.5–0.1 cm. Hojas sésiles, láminas de 0.7–0.85 × 0.3–0.4 cm, 3- ó 5-partidas a bipinnatipartidas, triangulares, híspidas a estrigosas en ambas superficies, lóbulos lineares, el medio de 8 mm, los laterales de 4 mm, ápices obtusos, márgenes algo revolutos. Inflorescencia en monobotrios. Florescencias en espigas densas, multifloras (a veces 2 ó 3 flores), raquis algo alargado en la fructificación; entrenudo basal de 1–2 cm; brácteas de 1.5–2 mm, triangulares, superficie abaxial pilosa a estrigosa, margen ciliado. Flores con cáliz de 7–8 mm, cilíndrico, híspido en la mitad superior y estrigoso en la mitad inferior, dientes del cáliz de 0.5–1 mm, triangulares; corola de 12 mm, violeta, azulada, rosada, glabra exteriormente, fauce pubescente; par superior de estambres con apéndices conectivales conspicuos, superando las tecas y sobrepasando la garganta corolar; estilo de 7.5–8 mm. Clusas de 4 mm long., cilíndricas, ápice apiculado, base no angostada y con repliegue basal y transversal de la pared comisural; superficie externa reticulada, superficies internas lisas.

Distribución geográfica y hábitat. *Glandularia andalgalensis* es endémica del Departamento Andalgalá de la provincia de Catamarca en Argentina, crece entre los 2700 y los 2900 m.

Observaciones. *Glandularia andalgalensis* pertenece al género *Glandularia* por ser de hábito rastrero, con conectivo de menor longitud que las tecas, apéndices conectivales desarrollados, estilo más de tres veces la longitud del ovario, inflorescencia en monobotrios y corola hipocraterimorfa; es sobre esta base que se transfiere esta especie del género

Verbena al género *Glandularia*. *Glandularia andalgalensis* es afín a *G. microphylla* y *G. sulphurea* por la división de la lámina foliar, la pubescencia híspida, la presencia de apéndices conectivales superando la longitud de las tecas y las clusas menores a 4 mm long.; se diferencia porque *G. microphylla* y *G. sulphurea* son sufrútices, tienen hojas pecioladas, brácteas ovadas y clusas con ápice obtuso.

Sólo se han podido estudiar dos ejemplares: el material tipo y el ejemplar de *Herrera 158* (SI). El ejemplar tipo fue determinado por Moldenke en un primer momento como *Verbena dissecta* Willd. ex Spreng., de la cual se diferencia claramente por el alargamiento del raquis en la fructificación.

Material adicional examinado. ARGENTINA. **Catamarca:** Dpto. Andalgalá, sobre ruta 47, ca. la intersección con el Río Ingenio o Potrerillos, *Herrera 158* (SI).

2. Glandularia andina (Griseb.) P. Peralta, comb. et stat. nov. Basiónimo: *Verbena erinoides* Lam. var. *andina* Griseb., Abh. Konigl. Ges. Wiss. Gottingen 19: 241. 1874. TIPO: Argentina. Catamarca: Vayas Altas, alpen von Belén, ene. 1872, *P. G. Lorentz 597* (holotipo, GOET no visto, GOET foto SI!; isotipos, CORD no visto, CORD foto SI!).

Glandularia santiaguensis Covas & Schnack, Revista Argent. Agron. 11: 92, fig. 2. 1944, syn. nov. *Verbena santiaguensis* (Covas & Schnack) Moldenke, Phytologia 2: 150. 1946. TIPO: Argentina. Santiago del Estero: camino entre Santiago del Estero y Catamarca, 1 abr. 1944, *B. J. C. Schnack 2111* (holotipo, SI 3808!).

Hemicriptófito rastrero, ramas floríferas ascendentes, radicantes en la base; ramas estrigosas con tricomas simples orientados hacia la base; entrenudos de 2–4 cm. Hojas con pecíolo de 0.5–1.7 cm, lámina de 2–5 × 1.5–3.5 cm, 5-sectada, lóbulos partidos a sectados, de contorno ovado-triangulares estrigosas en ambas, lóbulos de ápice agudo y margen revoluto. Inflorescencia en pleiobotrios heterotéticos o monobotrios. Florescencia en espigas densas multifloras, raquis algo alargado en la fructificación; entrenudo basal de 5–60 mm; brácteas de 3–4 mm, angostamente ovadas, superficie abaxial estrigosa, ciliadas en el margen. Flores con cáliz de 5–6.5 mm, estrigoso a híspido, dientes ca. 1 mm, aristados; corola de 8.5–9 mm, escasamente pubescente en el exterior del tubo y sobre los lóbulos, lila claro; par superior de estambres con apéndices conectivales, inclusos o no, superando la longitud de las tecas; estilo de 6 mm. Clusas de 2 mm, cilíndricas, rectas, ápice redondeado, base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa reticulada, superficie interna lisa.

Iconografía. Covas y Schnack (1944: 93, fig. 2), sub *Glandularia santiaguensis*.

Nombre vulgar. Malva de vaca, en *Biurrum 427* (SI).

Usos. Se la considera buena forrajera para ganado lechero, del ejemplar *Salas, J. C. s.n.* (SI).

Distribución geográfica y hábitat. Glandularia andina habita en las provincias del centro-norte de Argentina. Crece en bordes de camino, pastizales y campos, entre los 400 y 4000 m.

Observaciones. La descripción original de *Glandularia andina* se basa en un ejemplar cultivado a partir de semillas traídas de Santiago del Estero y cultivadas en Mendoza.

Glandularia andina es similar a *G. tomophylla* por la pubescencia del cáliz, tamaño de las clusas y apéndices conectivales; ambas se diferencian porque *G. tomophylla* presenta la lámina con los 2/3 superiores lobado y 1/3 basal sectado, híspida en la superficie abaxial y las brácteas de mayor tamaño. Puede ser confundida además con *G. cabrerae* y *G. cheitmaniana*, por la división sectada de las hojas; éstas últimas se diferencian principalmente por presentar un hábito erecto y por los apéndices conectivales breves no superando las tecas.

Material adicional examinado. ARGENTINA. **Catamarca:** Dpto. El Alto, Tapso, al lado del FC, *Boelcke s.n.* (SI); Dpto. La Paz, entre Recreo y Paso Cruz, ruta prov. 20, *Troncoso 1755* (SI); Dpto. Pomán, s. loc., *Biloni 6247* (SI). **Chaco:** Dpto. Gral. Güemes, 1 km de Castelli en dirección E, por ruta que une Castelli–El Asustado, *Fortunato 1274* (SI). **Córdoba:** Dpto. Cruz del Eje, Soto, *Nicora 17911* (SI); Dpto. Ischillín, entre Avellaneda y Los Pozos, *Hunziker s.n.* (SI); Dpto. Punilla, San Esteban, *Nicora 1526* (SI); Dpto. Río Primero, entre la Estación La Posta y Cañada Honda, *Sayago 2132* (SI); Dpto. Río Seco, Sebastián Elcano, *Luti 4104* (SI). **Formosa:** Dpto. Bermejo, entre Fortín Pilcomayo y Bajo Hondo, *Cordini 17* (SI). **La Rioja:** Dpto. Chamical, entre Santa Lucía y el empalme con ruta nac. 79, *Biurrum 235* (SI); Dpto. Gral. Belgrano, ruta nac. 79, cantera de Lajas, a unos 10 km de Olta, rumbo a Olpas, *Pagliari 804* (SI). **Salta:** Dpto. Cachi, Cuesta del Obispo, Piedra del Molino, *Cabrera 30726* (SI); Dpto. Chicoana, Cuesta del Obispo, *Cabrera 22009* (SI); Dpto. Gral. Güemes, Río Juramento, junto al camino, *Cabrera 29965* (SI); Dpto. Iruya, camino a Iruya, *Kiesling 3573* (SI); Dpto. La Viña, ruta nac. 68, 6 km al S de La Viña, camino a Cafayate, *Zuloaga 7888* (SI); Dpto. Metán, ruta nac. 34, 78 km N de Metán, *Cordo s.n.* (SI); Dpto. Rosario de la Frontera, ruta nac. 34, pocos km N de Rosario de la Frontera, *Burkart 30581* (SI). **San Luis:** Dpto. Gdor. Dupuy, La Mira Pampa, *Cano 2629* (SI); Dpto. La Capital, Alto Pencoso, *Hunziker, J. H. 6467* (SI). **Santiago del Estero:** Dpto. Capital, Ciudad, campo ca. Río Dulce, *Ulibarri 1013* (SI); Dpto. Copo, Monte

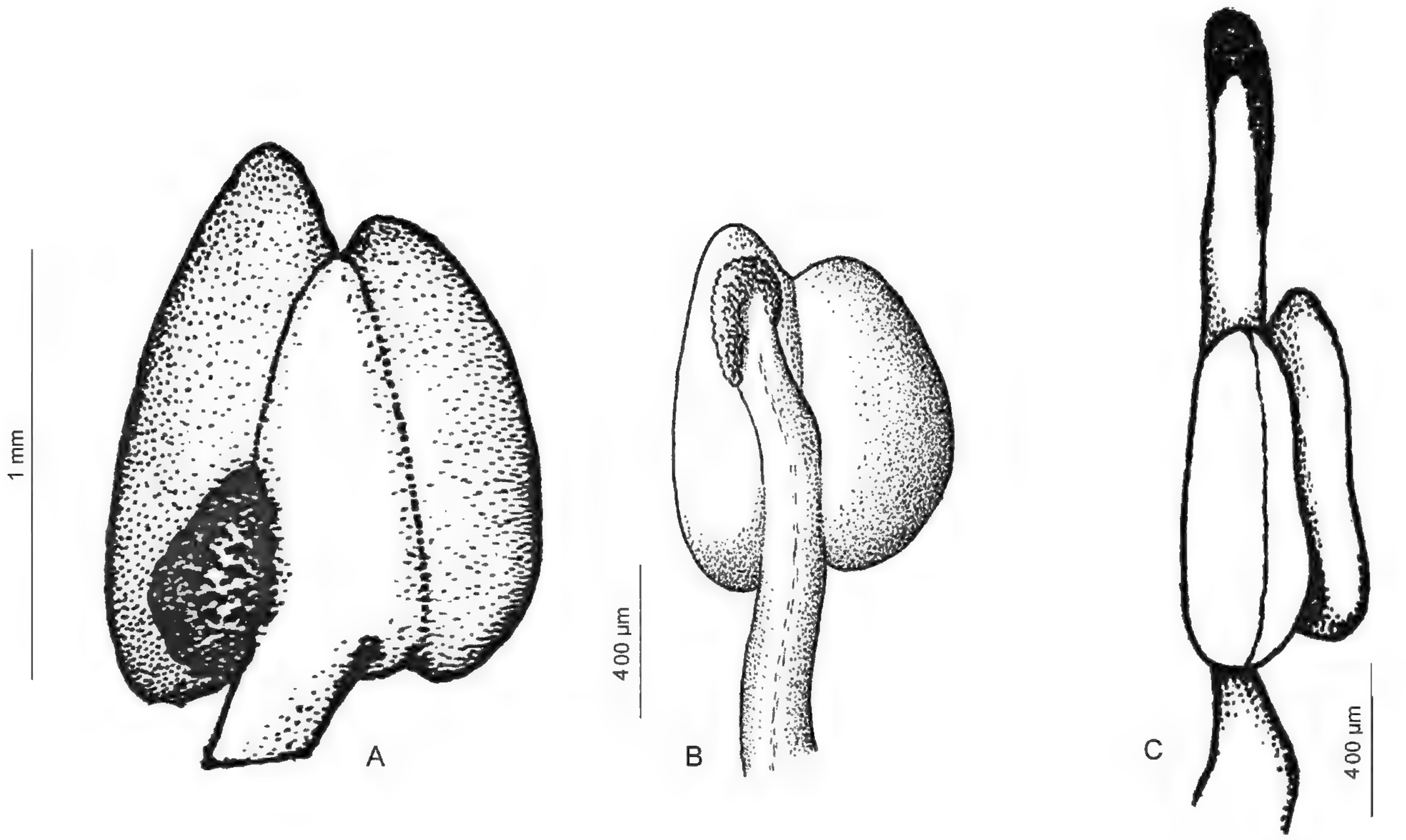

Figura 1. Morfología de los estambres. —A. *Glandularia megapotamica* (Spreng.) Cabrera & G. Dawson, de *Burkart 30103* (SI). —B. *G. cabrerae* (Moldenke) Botta, de *Burkart 30591* (SI). —C. *G. selloi* (Spreng.) Tronc., dibujo tomado de Troncoso (1964: 483, fig. 6J).

Quemado, *Rotman 990* (SI); Dpto. Guasayán, de Santa Catalina a Guampacha, *Rotman 252* (SI); Dpto. Jiménez, El Fisco, 40 km NNW de Pozo Hondo, R 34, *Krapovickas 30520* (CTES, SI); Dpto. La Banda, La Isla, *Walmich 2244* (SI); Dpto. Ojo de Agua, Piedra Blanca, *Cabrera 31889* (SI); Dpto. Quebrachos, Sur de Sumampa, *Bartlett 19862* (SI); Dpto. Río Hondo, ruta nac. 9, Naranjito, *Zuloaga 8420* (SI); Dpto. Robles, Vilmer, *Maldonado 419* (SI); Dpto. Taboada, Ea. La Candelaria, *Denalpfi 28* (CTES). **Tucumán:** Dpto. Capital, Villa Luján, *Venturi 4* (SI); Dpto. Chicligasta, Ea. Santa Rosa, *Venturi 4762* (SI); Dpto. Cruz Alta, Las Cejas, *Venturi 2303* (SI); Dpto. Graneros, La Cocha, *Burkart 26600* (SI); Dpto. Trancas, Tapia, *Venturi 1042* (SI).

3. Glandularia araucana (Phil.) Botta, Parodiana 8: 26. 1993. Basiónimo: *Verbena araucana* Phil., Anales Univ. Chile 43: 520. 1873. TIPO: Chile. Cupulhue, en la Araucanía, s.d., *J. Volkmann s.n.* (lectotipo, designado por Botta [1993: 26], SGO 42473! [código de barras SGO 00004243]; isotipo, SGO 54770! [código de barras SGO 00004244], SGO foto SI!).

Verbena chilensis Moldenke, Known Geogr. Distrib. Verb. Avicenn. 78. 1942. Nombre reemplazado para *Verbena glabrata* Phil., Anales Univ. Chile 36: 190. 1870, nom. illeg., non *Verbena glabrata* Kunth, 1818. TIPO: "Argentina? Iter Mendocinum", 1868–1869, *Philippi s.n.* (lectotipo, designado por Botta [1993: 26], SGO 54790! [código de barras SGO 4254]; isotipos, GOET no visto, SGO 42446! [código de barras 4255]).

Sufrútice de 25–30 cm, ramificado, ramas glabras, apoyantes, formando matas; ramas floríferas erectas; entrenudos de 7–10 mm. Hojas con pecíolo de 5–7 mm; lámina de 2–3.5 × 1–2 cm, contorno angostamente ovado, 3-lobadas, 3- ó 5-partidas a bipinnatípartidas, raro enteras, glabras, lóbulos ovados a filiformes, de 1.5–4.5(–5.5) mm lat., margen entero. Inflorescencias en pleiobotrios heterotético, con paracladios bracteosos superando o no la florescencia principal, o en monobotrios. Florescencias en espigas multifloras, densas, raquis algo alargado en la fructificación; entrenudo basal desarrollado, 2–7.5 cm; brácteas de (2–)3–4 mm, ovadas, margen ciliado. Flores con cáliz de 9–10.5 mm, hispídulo, a veces sólo en la base; dientes abaxiales ca. 1 mm; corola de (10–)17–23 mm, amarillo claro, tubo de 14–20 mm, superficie externa glabra, fauce pubescente, lóbulos de 3–3.5 mm; par superior de estambres con apéndices conectivales oscuros, claviformes, conspicuos, sobrepasando la garganta corolar; estilo de 16 mm. Clusas de 4–5 mm, subcilíndricas, ápice obtuso y base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa pardo obscura, reticulada y las internas con escasas papilas o sin ellas.

Iconografía. Botta (1993: 27, fig. 7A–L), sub *Glandularia araucana*.

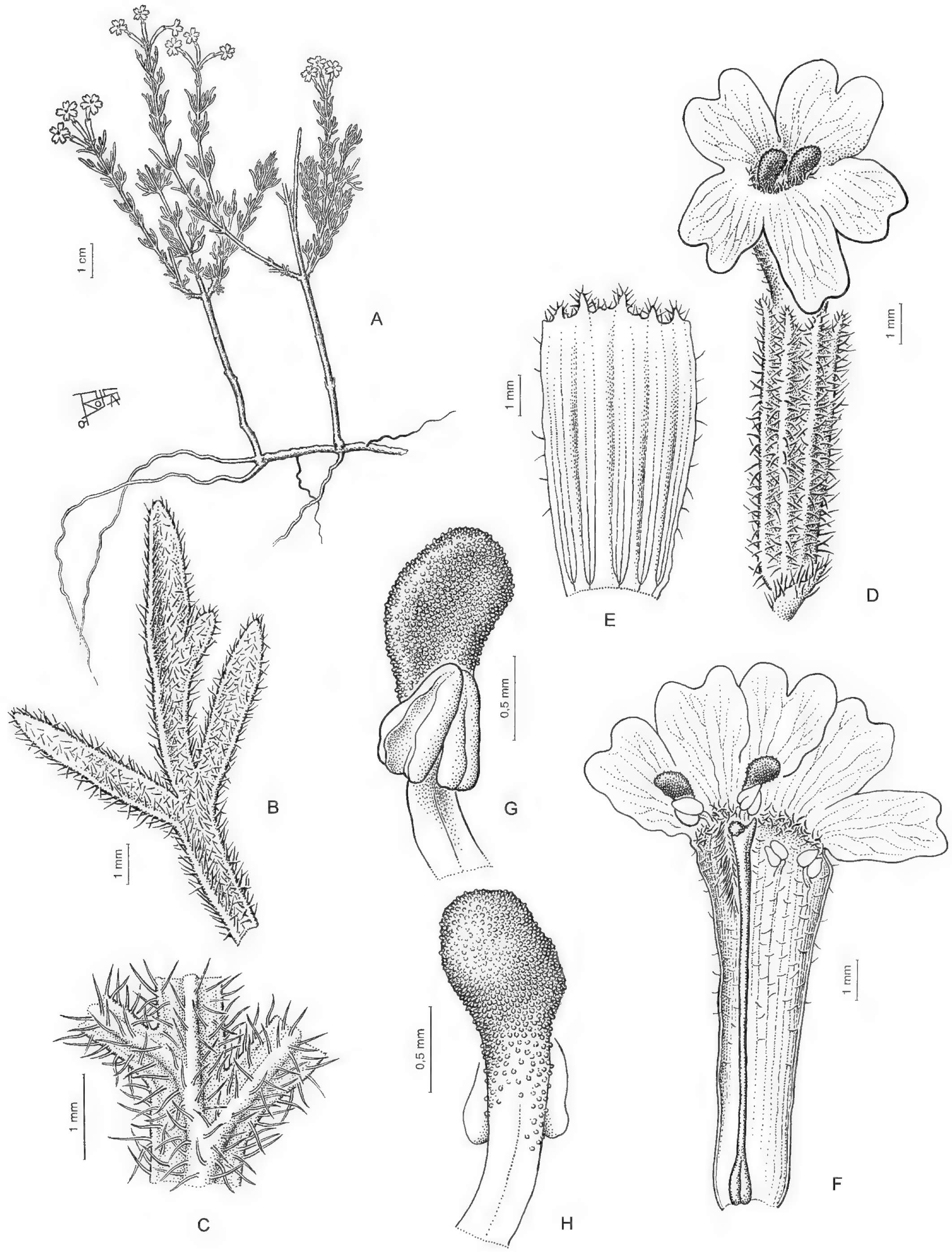

Figura 2. *Glandularia andalgalensis* (Moldenke) P. Peralta. —A. Aspecto general. —B. Hoja cara adaxial. —C. Detalle de la pubescencia de la hoja. —D. Flor y bráctea. —E. Cáliz expandido. —F. Corola abierta mostrando la disposición de los estambres y la longitud del estilo. —G, H. Detalles de los estambres, vistas dorsal y ventral, respectivamente. A–H de *Herrera 158* (SI).

Distribución geográfica y hábitat. *Glandularia araucana* crece al oeste de la Argentina, desde las provincias de San Juan hasta Chubut en el sur; también crece en Chile. Habita entre 900 y 3150 m, sobre suelos rocosos, pedregosos, áridos y laderas de montañas.

Observaciones. Los ejemplares de la provincia de San Juan de la loc. de Sierra de Pié de Palo (Argentina), son de porte más pequeño y más achaparrados.

En algunos ejemplares (e.g., *Troiani 15813*, CTES, SI) los paracladios pueden ramificarse dando paracladios de primer orden con las mismas características que los anteriores. Las flores presentan un suave aroma.

Moldenke (1942b), funda *Verbena chilensis* como un nuevo nombre para *V. glabrata* Phil., esta última es ilegítima por ser un homónimo posterior. El tipo de este taxón, fue depositado en B (B foto F 17417 en SI!) actualmente destruido, por esta razón Botta (1993) designa un lectotipo.

Glandularia araucana es muy similar a *G. aurantiaca* y *G. flava*, por el hábito, color de la corola y pubescencia; las últimas se diferencian principalmente por los apéndices conectivales de menor tamaño y porque las divisiones de la lámina foliar nunca llegan a ser bipinnatipartidas.

Material adicional examinado. ARGENTINA. **Chubut:** Dpto. Escalante, Norte de Comodoro Rivadavia, *Garaventa 5759* (CONC); Dpto. Sarmiento, 29 km W de Sarmiento Sa. San Bernardo, *Sanchéz 300* (CTES); Dpto. Telsen, camino entre Gan Gan y Caín, *Bartoli 98/02–2* (CTES). **Mendoza:** Dpto. Las Heras, betw. Villavicencio & Uspallata, *Böcher 2138* (SI); Dpto. Lavalle, Cruz de Los Paramillos, *Nicora 4351* (SI); Dpto. Malargüe, Reserva Prov. La Payunia, Pampas Negras, *Prina 1743* (CTES, SI); Dpto. San Rafael, Co. Nevado, laderas alrededores de La Cienaguita, *Boelcke 15675* (SI); Dpto. Tupungato, Arroyo de las Costadoras, *Ruíz Leal 3628* (SI). **Neuquén:** Dpto. Aluminé, subida de Catatrem, entre 1 de Mayo y Rahue, *Cabrera 18693* (LP, SI); Dpto. Catán Lil, Cerro Chachil, *Schajovskoy 154/IV* (SI); Dpto. Huiliches, La Rinconada, *Troiani 15813* (CTES, SI); Dpto. Lácar, 20 km N del nacimiento de ruta prov. 23, *Correa 10469* (SI); Dpto. Los Lagos, Nahuel Huapi Norte, *Garaventa, A. 5835* (CONC); Dpto. Minas, ruta prov. 43, 13 km al S de Andacollo, *Guaglianone 3236* (SI); Dpto. Pehenches, Cerro Auca Mahuida, *Mallo s.n. BAB 18521* (CTES); Dpto. Picunches, ruta nac. 22, Paso Pino Hachado, *Cocucci 2358* (CTES, SI); Dpto. Zapala, Laguna Blanca, *Cabrera 18687* (LP). **Río Negro:** Dpto. 25 de Mayo, Ingeniero Jacobacci, en cerros al E del pueblo, en yacimientos de tiza, *Seijo 2255* (CTES); Dpto. 9 de Julio, Meseta de Somuncurá, Cerro Corona, *Troiani 15107* (CTES, SI). **San Juan:** Dpto. Angaco, Sierra de Pié de Palo, camino a Mogote de los Corralitos, ca. la antena, *Kiesling 3127* (SI); Dpto. Caucete, Mogote Corralitos, Sierra de Pié de Palo, *Haene 1078* (SI); Dpto. Sarmiento, Quebrada del Río de Los Sombreros, *Kiesling 4214* (SI). CHILE. **IV Región:** Limarí, *Philippi s.n.* (SI). **IX Región:** Malleco, Liucura, Lonquimay, *Behn 8031* (CONC).

4. Glandularia aristigera (S. Moore) Tronc., Darwiniana, 14: 636. 1968. Basiónimo: *Verbena aristigera* S. Moore, Trans. Linn. Soc. London, Bot., ser. 2, 4(3): 439. 1895. TIPO: Brazil. Mato Grosso do Sul: "prope montem Pão d'Assucar dictum, inter Coimbrá et fl. Apa", 1891–1892, *S. Moore 1083* (lectotipo, aquí designado, BM 0070617!, BM foto SI!; isotipos, G no visto, SI 3677!).

Verbena tenuisecta Briq., Annuaire Conserv. Jard. Bot. Genève 7–8: 294. 1904. *Glandularia tenuisecta* (Briq.) Small, Man. S. E. Fl. (Small): 1139. 1933. TIPO: Paraguay. La Trinidad, 4 oct. 1875, *B. Balansa 1025* (holotipo, G no visto, G foto SI!; isotipos, F 0074536!, K 00470520!, K foto SI!, NY 0138336!, NY foto SI!, P 00650869!, SI!).

Hemicriptófito rastrero de 20–60 cm alt., ramas floríferas extendidas, glabrescentes o estrigosas, más densamente hacia el ápice; entrenudos de 2–3.5 cm. Hojas con pecíolo de 5–8 mm, lámina de 1–3 × 1.5–3 cm, contorno oval a triangular, 3-sectas, bipinnatisectas o tripinnatisectas, superficie adaxial estrigosa, superficie abaxial estrigosas sobre la vena media, resto de la lámina glabra, margen de los lóbulos entero extendido o revoluto. Inflorescencia principalmente en monobotrios, menos común inflorescencias en pleiobotrios heterotéticos con 1 par de paracladios bracteosos u frondosos sobrepasando la florescencia principal. Florescencias en espigas multifloras, densas, raquis alargado en la fructificación; entrenudos basal desarrollado, 10–70 mm; pedicelo ca. 1 mm; brácteas de 3–3.5 mm, oval a angostamente ovada, estrigosa, más densamente hacia la base, ápice atenuado. Flores con cáliz de 9–10 mm, pubescencia densa, cano-estrigosa, con escasas glándulas pateliformes, dientes desiguales, el menor de 0.5 mm y el mayor de 1 mm, filiformes, conniventes en la fructificación; corola de 12 mm, glabra externamente, fauce pubescente, rosada, lila o violeta, lóbulos de 4–4.5 mm; par superior de estambres con apéndices conectivales pequeños, no superando las tecas, inclusos; estilo de 8.5–9 mm. Clusas de 3 mm, cilíndricas, ápice obtuso, base no angostada y con repliegue basal y transversal de la pared comisural, pardas, superficie externa reticulada hacia el ápice, zona basal lisa, superficie interna papilosa.

Iconografía. Troncoso (1964: 477, fig. 4), sub *Glandularia tenuisecta*; Troncoso y Botta (1993: 109, fig. 49), sub *G. aristigera*.

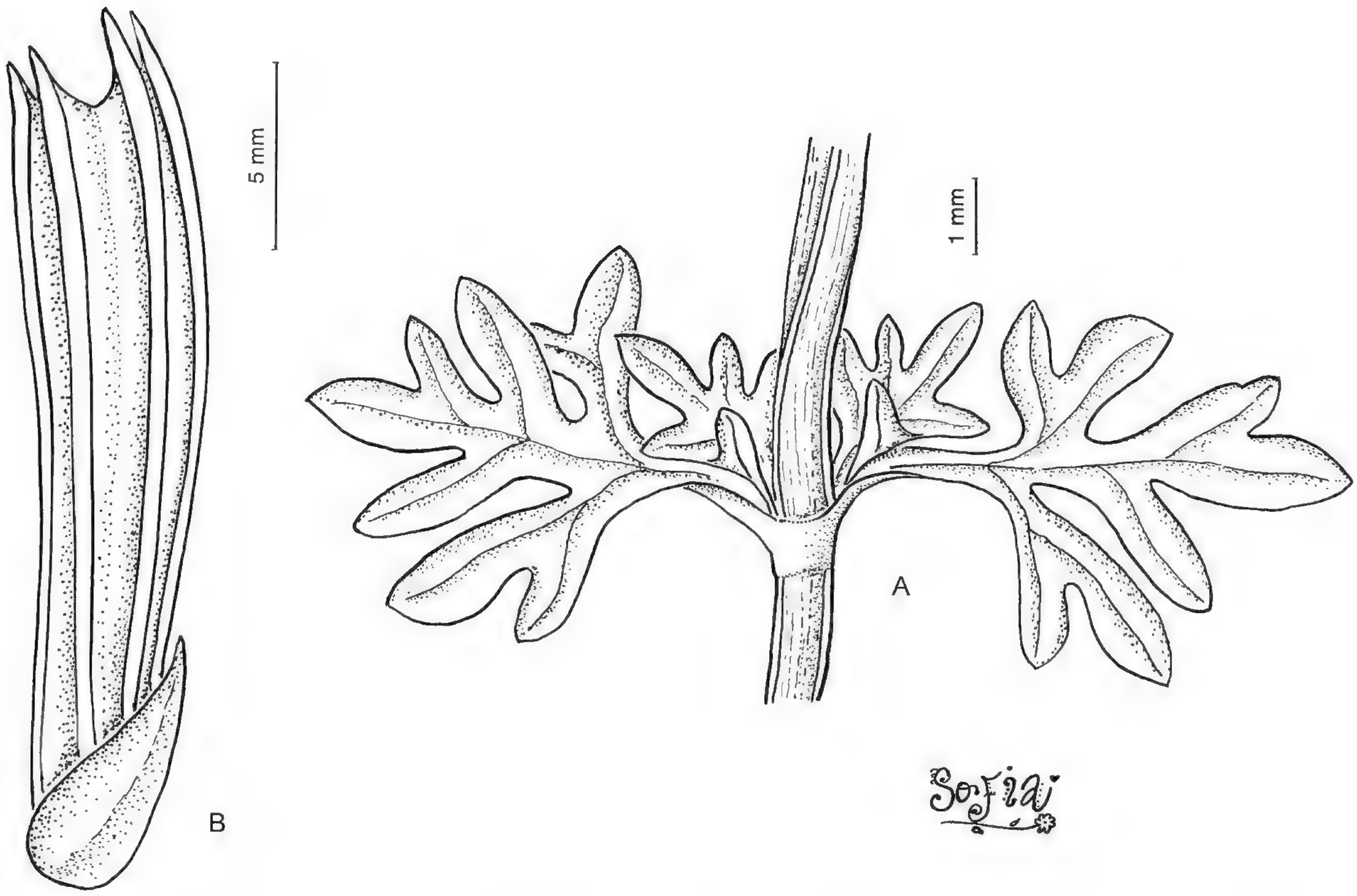

Figura 3. *Glandularia aurantiaca* var. *glabra* (Hicken) P. Peralta. —A. Detalle de la inserción foliar. —B. Cáliz y bráctea. A, B de *A. Ruíz Leal & F. A. Roig 15723* (SI).

Nombre vulgar. Yerba meona, Malaq lawogo, Tapo lawogo, en ejemplar de *Vuoto s.n. BACP 2049* (LP); Margarita celeste, en el ejemplar *Sturzenegger 3048* (SI).

Distribución geográfica y hábitat. Glandularia aristigera crece al norte, noreste y centro de la Argentina; también en suroeste de Bolivia (Cochabamba, Santa Cruz), en tres estados del sur de Brasil (Mato Grosso, Paraná y Rio Grande do Sul) y en los departamentos del norte, centro y sur de Paraguay; probablemente también crezca en Uruguay. Habita en zonas abiertas, modificadas, bordes de camino, suelos arenosos, lugares húmedos, afloramientos rocosos, hasta los 1250 m.

Fenología. Glandularia aristigera florece de octubre a marzo, aunque puede llegar la floración a mayo.

Observaciones. El holotipo de esta especie depositado en B está destruido (B foto F 17403 en SI!). Por tal motivo se elige como lectotipo el isotipo depositado en el herbario BM, por ser el más completo según notas de la Sra. Nélida Troncoso y corresponderse con el protólogo.

El ancho de los lóbulos foliares es un carácter muy variable, a veces son angostos como los presentes en la especie afín *Glandularia tenera*, de la cual se diferencia principalmente por el ápice rostrado de las clusas, los dientes subulados del cáliz y los apéndices conectivales delgados que superan la longitud de las tecas.

Material adicional examinado. ARGENTINA. **Chaco:** Dpto. 1° de Mayo, Colonia Benítez, *Schulz 268* (CTES); Dpto. 12 de Octubre, 14 km W de Gral. Pinedo, ruta prov. 94, *Krapovickas 17315* (SI); Dpto. Bermejo, Las Palmas, *Schulz 2888* (CTES); Dpto. San Fernando, entrada a Resistencia a orillas del Río Negro, *Díaz s.n.* (SI); Dpto. Tapenaga, Villa Ángela, *Rodrigo 2668* (SI). **Córdoba:** Dpto. Gral. San Martín, Villa María, *Hicken 308* (SI). **Corrientes:** Dpto. Capital, 5 km E de Laguna Brava, *Krapovickas 15910* (SI); Dpto. Curuzú-Cuatiá, Curuzú-Cuatiá, *Martínez Crovetto 8400* (SI); Dpto. Gral. Paz, Lomas de Vallejos, *Schinini 7011* (CTES, SI); Dpto. Goya, ruta nac. 126, 2 km N de ayo. Batelito, *Krapovickas 22730* (SI); Dpto. Ituzaingó, 15 km E de ruta nac. 12, camino a San Carlos, *Krapovickas 18053* (CTES, SI); Dpto. Monte Caseros, Orillas arroyo Timboí, *Nicora 4956* (SI); Dpto. San Martín, Carlos Pelegrini, 8 km al N, ruta nac. 14, *Krapovickas 20129* (SI); Dpto. San Miguel, ruta nac. 12, 24 km E de Km 1111, *Krapovickas 14872* (SI, CTES); Dpto. Santo Tomé, Arroyo Chimiray, *Krapovickas 26143* (SI). **Entre Ríos:** Dpto. Colón, Palmar de Colón, sobre ruta nac. 14, *Troncoso 3767* (SI). **Formosa:** Dpto. Formosa, alrededores de la ciudad, *Guaglianone 301* (SI); Dpto. Patiño, El Descanso, *Filipov 53* (SI); Dpto. Pilagá, *Vuoto s.n. BACP 2049* (LP); Dpto. Pilcomayo, Siete Palmas, *Rojas 9011* (SI); Dpto. Pirané, Pirané, *Pierotti 72839* (SI). **Jujuy:** Dpto. Doctor Manuel Belgrano, s. loc.,

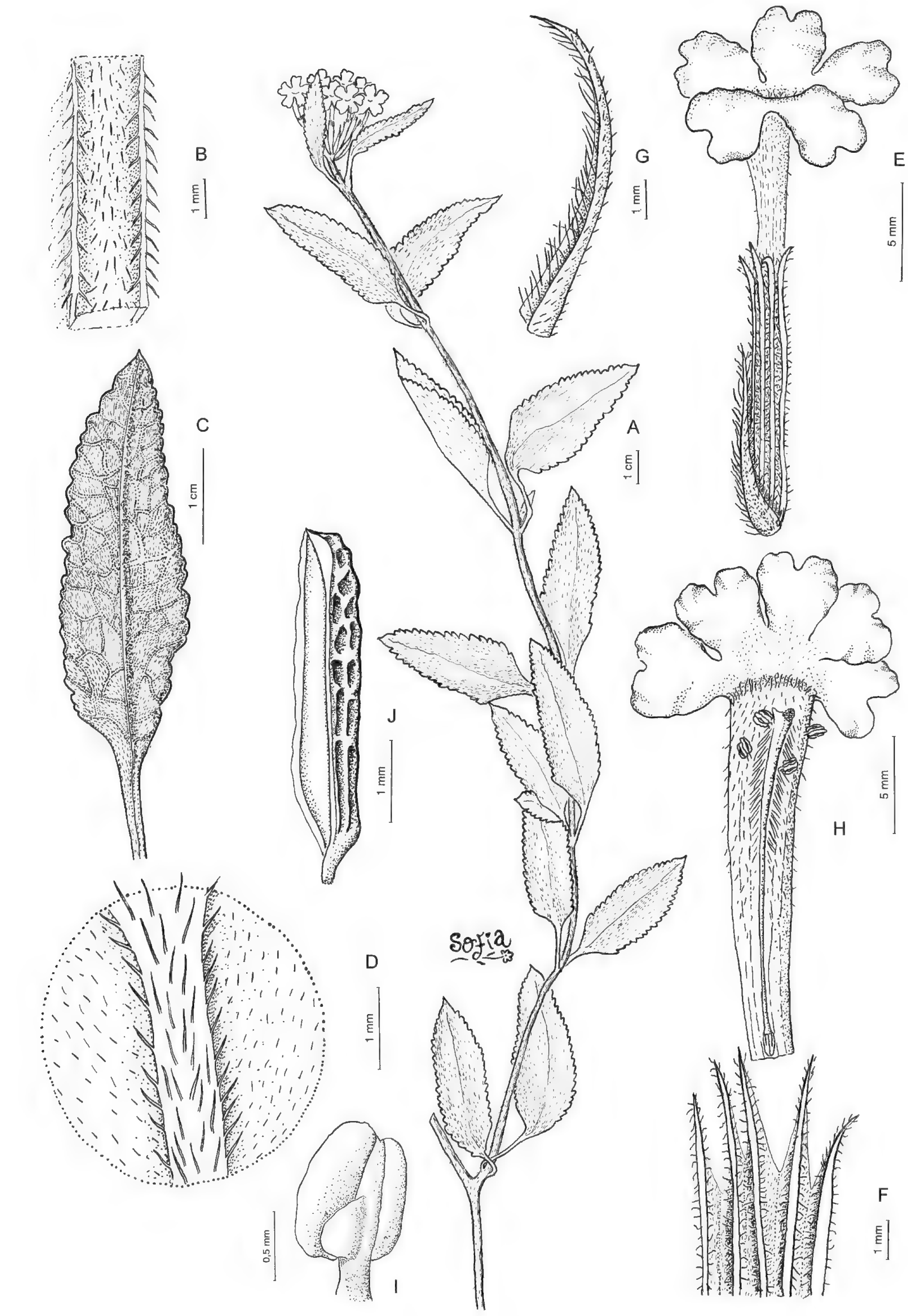

Figura 4. *Glandularia hassleriana* (Briq.) Tronc. —A. Aspecto general. —B. Detalle de la pubescencia del tallo. —C. Hoja, superficie adaxial. —D. Detalle de la hoja, superficie abaxial. —E. Flor y bráctea. —F. Detalle de los dientes del cáliz. —G. Bráctea. —H. Corola expandida mostrando la inserción de los estambres y el gineceo. —I. Detalle de los estambres en vista dorsal. —J. Clusa. A–J de *Krapovickas 21608* (SI).

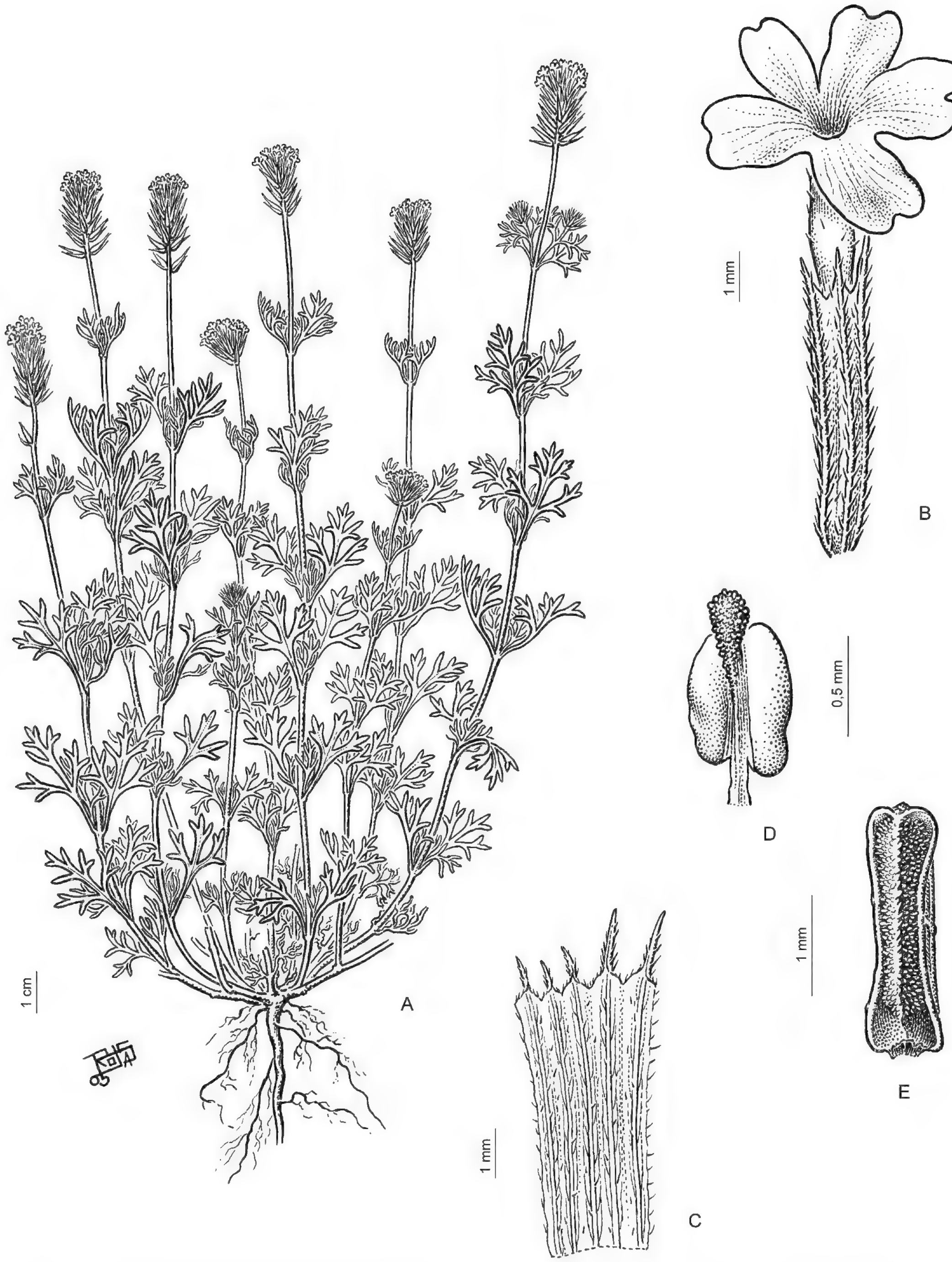

Figura 5. *Glandularia mendocina* (Phil.) Covas & Schnack. —A. Aspecto general. —B. Flor. —C. Cáliz expandido. —D. Detalle del estambre. —E. Clusa, vista ventral. A–E de *Roig 8151* (SI).

Cabrera 27469 (SI); Dpto. Ledesma, s. loc., *s. coll. s.n.* (LP). **Misiones:** Dpto. Apóstoles, ruta prov. 203, entre ruta nac. 14 y ruta prov. 1, *Cabrera 29180* (SI); Dpto. Cainguás, Predio UNLP, Reserva Valle del Arroyo Cuña Pirú, picada desde la Est. Biológica hasta arroyo Liso, *Biganzoli 1463* (SI); Dpto. Candelaria, Cerro Corá, *Krapovickas 16015* (CTES, SI); Dpto. Capital, 5 km al W de Posadas, *Hunziker 9963* (SI); Dpto. Concepción, 2.5 km de Santa María, camino a San Javier, *Morrone 599* (CTES, SI); Dpto. Iguazú, Victoria, *Montes 15477* (SI); Dpto. Ldor. Gral. San Martín,

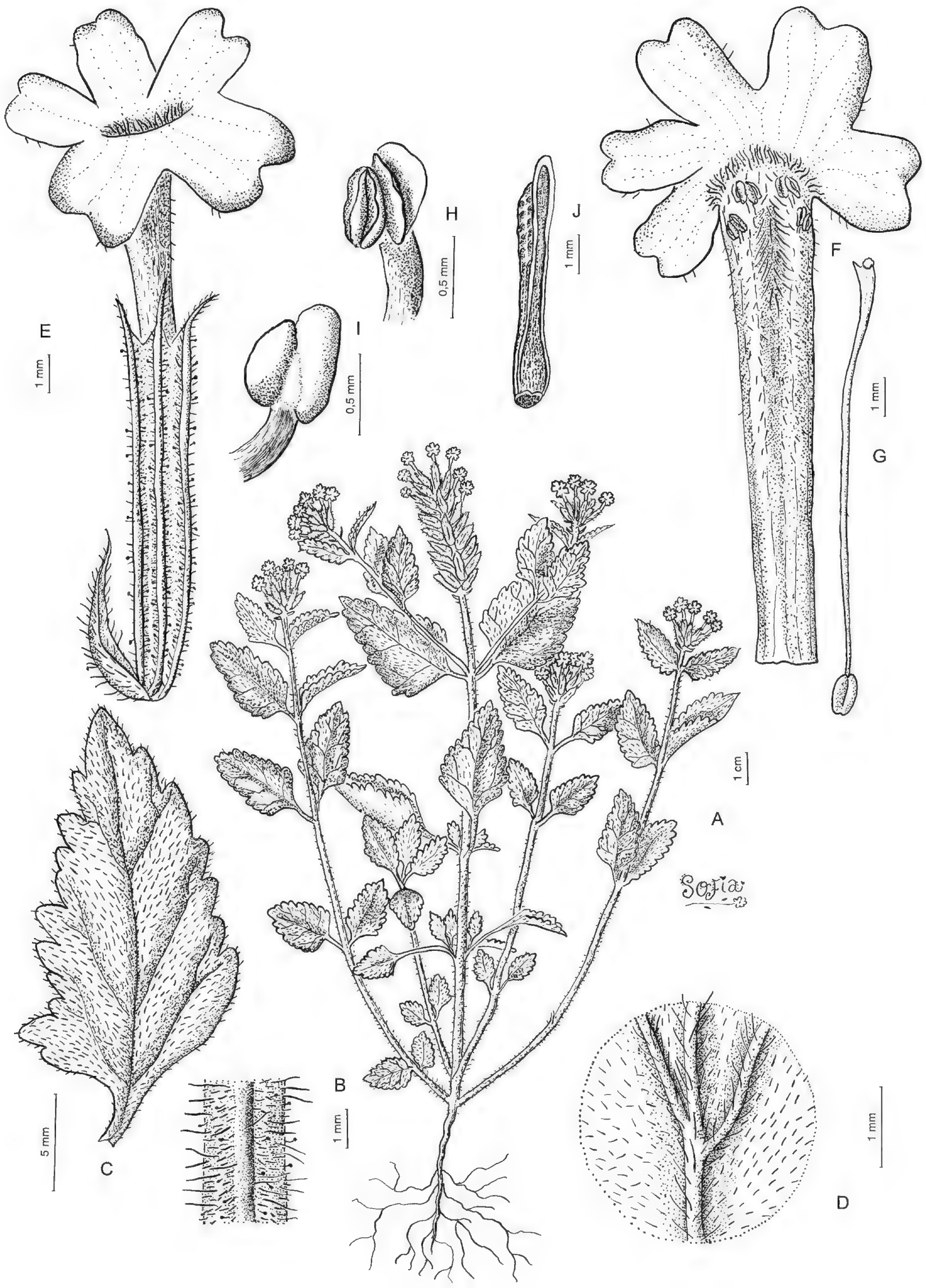

Figura 6. *Glandularia nana* (Moldenke) Tronc. —A. Aspecto general. —B. Detalle de la pubescencia del tallo. —C. Hoja, superficie adaxial. —D. Detalle de la hoja, superficie abaxial. —E. Flor y bráctea. —F. Corola expandida mostrando la pubescencia y la inserción de los estambres. —G. Estilo y ovario. —H. Estambre vista ventral. —I. Estambre vista dorsal. —J. Clusa. A–J de *Martínez 9693* (SI).

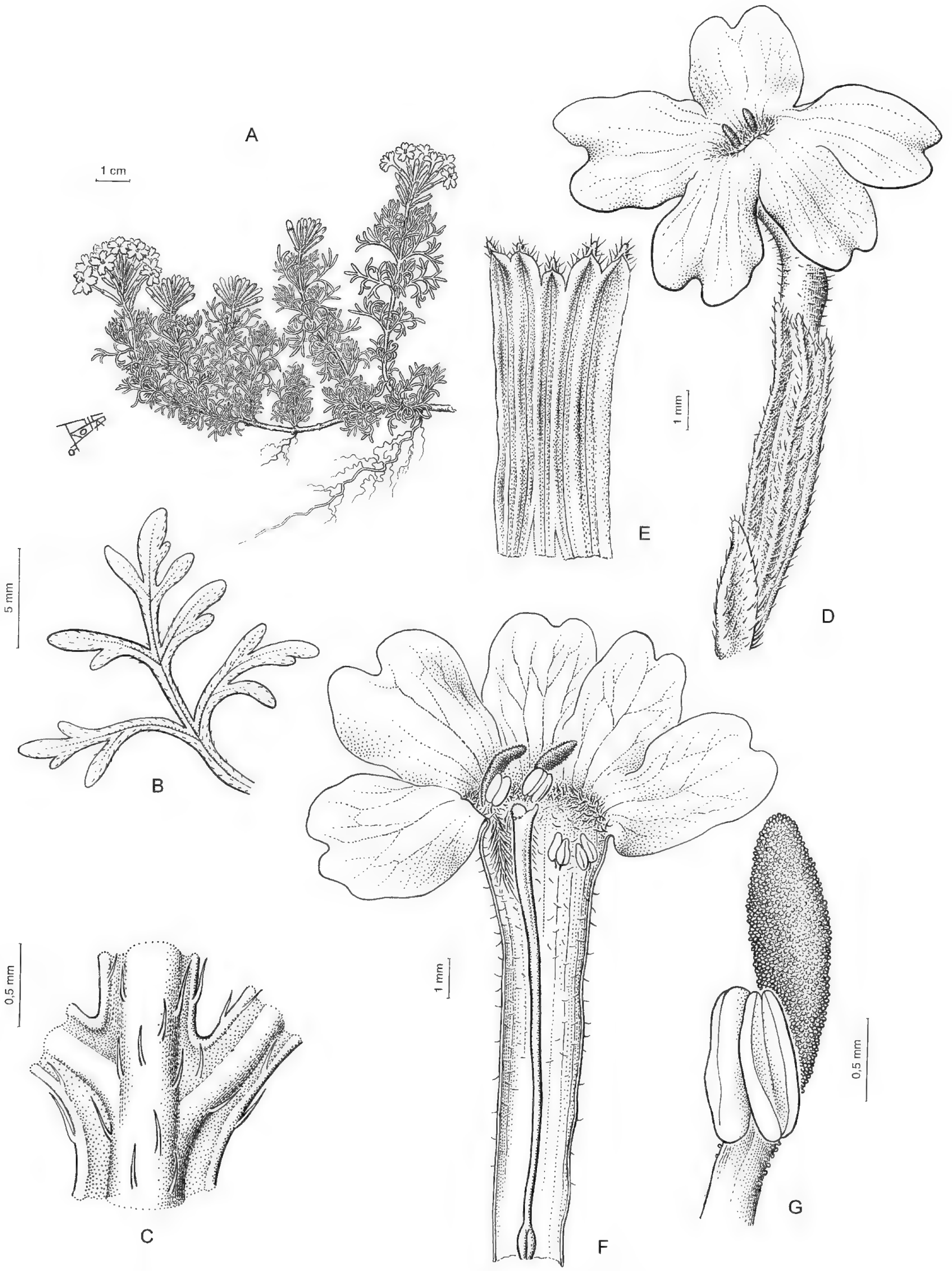

Figura 7. *Glandularia radicata* (Moldenke) Tronc. ex Múlgara. —A. Aspecto general. —B. Hoja, superficie adaxial. —C. Detalle de la hoja, superficie abaxial. —D. Flor y bráctea. —E. Cáliz desplegado. —F. Corola abierta mostrando la disposición de los estambres y la longitud del estilo. —G. Detalle del estambre. A–G de *Ruíz Leal 26329* (SI).

Puerto Rico, *Montes 3988* (CTES); Dpto. San Ignacio, desvío a Colonia Alberdi, 5 km ruta 14, *Múlgura 1722* (CTES, SI); Dpto. San Javier, San Javier, ca. Matadero, *Hunziker 9950* (SI); Dpto. San Pedro, ruta prov. 16, 2 km ruta nac. 14, *Múlgura 4042* (SI). **Salta:** Dpto. Cafayate, 89 km N de Cafayate, *Cordo s.n.* (SI); Dpto. Capital, ciudad de Salta, vías del FFCC, playa de maniobras entre la estación y molino Batuel, *Novara 8244* (SI). **Santa Fé:** Dpto. San Javier, S de Alejandra, *Martínez Achenbach 1000* (SI). **Santiago del Estero:** Dpto. Capital, alrededores de Santiago del Estero, orillas Río Dulce, *Ulibarri 1780* (SI). **Tucumán:** Sin dpto., terrenos de la Estación Experimental Agrícola, *Burkart 17570* (SI). BOLIVIA. **Cochabamba:** Campero, 5 km de Aiquile sobre el camino hacia Puente Arce, *Saravia 993* (SI). **Santa Cruz:** Del Cercado, *Steinbach 2533* (SI). **Tarija:** O'Connor, 13 km W camino a Tarija, *Marazzi, B. BM265* (SI, Z). BRASIL. **Mato Grosso:** Rio Brilhante, Rio das Araras, *Hatschbach 25241* (SI). **Paraná:** Guarapuava, Rio Iguaçu, Barra do Jordão, *Hatschbach 9946* (SI). **Rio Grande do Sul:** Caaró S. Luiz, *Rambo 53317* (SI). PARAGUAY. **Alto Paraguay:** San Salvador, *Rojas 2528* (SI). **Boquerón:** Trail to Laguna Negra, *Zardini 59866* (SI). **Caaguazú:** Arroyo Yakare'í, along S side from ruta 2, *Zardini 10808* (SI). **Central:** Tavarory, along Arroyo Abaí, *Zardini 23024* (SI). **Concepción:** Chaco Paraguayo, El Pedernal, al S de Concepción, *Burkart 18389* (SI). **Cordillera:** Confluence of Río Paraguay and Río Salado, *Zardini 22263* (SI). **Guairá:** Colonia Independencia, *Schinini 1673* (CTES). **Itapúa:** Villa Encarnación, *Schrottky 15* (SI). **Misiones:** 12 km W de San Ignacio, camino a Pilar, *Arbo 1916* (CTES, SI). **Paraguarí:** Acahay Massif, easternmost peak of massif, *Zardini 16237* (SI). **Presidente Hayes:** Asunción, 333 km hacia Filadelfia, *Beck 7470* (SI).

5. Glandularia aurantiaca (Speg.) Botta, Parodiana 8(1): 29. 1993. Basiónimo: *Verbena aurantiaca* Speg., Revista Fac. Agron. Univ. Nac. La Plata 3: 563. 1897. TIPO: Argentina. Santa Cruz: "in Golfo de San Jorge", Feb 1896, *C. Ameghino s.n.* (lectotipo, aquí designado, LP 10404!, LP foto SI!; isotipo, SI 3680!).

Sufrútice 10–40 cm alt., ramas tetrágonas erectas o algo decumbentes, glabras; entrenudos de 0.5–1.5 cm. Hojas con pecíolo de 4–6 mm, lámina de 2–3 × 1–2 cm, 3-lobadas, 3-sectas, con lóbulos enteros o lobados, elípticos a espatulados, contorno ovado a angostamente ovado, ápice redondeado, subcrasas, superficies glabras o con tricomas cortos y rígidos, adpresos en el margen. Inflorescencia en pleiobotrios heterotéticos, 1 ó 2 pares de paracladios frondosos hacia la base o no, superando la florescencia principal, a veces con paracladios de primer orden. Florescencias en espigas multifloras, densas, raquis alargado en la fructificación; brácteas de 4.5–6.5 mm, las basales de mayor longitud, ovadas a ovado-angostas, ápice atenuado y rígido. Flores con cáliz de 9–10 mm, glabro o estrigoso hacia el ápice, dientes breves de 0.5–1 mm, subiguales; corola de 14–16.5 mm, amarillo pálido o rosadas; tubo glabro exteriormente, fauce pubescente; par superior de estambres con apéndices conectivales breves, inclusos, menores que las tecas; estilo de 10–14 mm. Clusas de 4–4.5 mm, pardo claras, ápice obtuso, base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa reticulada, superficie interna lisa.

Observaciones. En el protólogo Spegazzini (1897: 563), nombra dos ejemplares: "In pratis siccis sabulosis prope *Lago Argentino*, anno 1884, (T. F.) et in *Golfo de San Jorge*, Febr. 1896 (C. Ameghino)". En 1993, cuando hace la combinación Botta, no designa lectotipo, por tal motivo se realiza la lectotipificación en el presente trabajo. Se elige como lectotipo al último (feb. 1896, *C. Ameghino s.n.*, LP) porque es el ejemplar que mejor coincide con el protólogo de la especie y ser el más completo.

Clave de las Variedades de *Glandularia aurantiaca*

5a. Brácteas con margen ciliado y con escasos tricomas adpresos; cáliz estrigoso hacia el ápice ..... 5a. var. *aurantiaca*

5b. Brácteas con margen ciliado, resto glabra; cáliz glabro o con muy pocos tricomas cortos y dispersos..... 5b. var. *glabra*

5a. Glandularia aurantiaca var. **aurantiaca**.

Verbena aurantiaca Speg. f. *rosea* Moldenke, Phytologia 5: 342. 1956. TIPO: Argentina. Chubut: Dpto. Escalante, Comodoro Rivadavia, entre Estancia Pío Pío y Colonia Sarmiento, 17 dic. 1953, *A. Ruíz Leal 14703* (holotipo, NY no visto; isotipos, LL 375215!, LL foto SI!, SI!).

Hojas con superficies con tricomas cortos y rígidos, adpresos en el margen, en ocasiones en toda la superficie. Brácteas ciliadas en el margen resto de la superficie con tricomas adpresos; cáliz estrigoso hacia el ápice.

Iconografía. Botta (1993: 29, fig. 8), sub *Glandularia aurantiaca*.

Distribución geográfica y hábitat. Glandularia aurantiaca crece en Argentina, desde el sur de Mendoza hasta Santa Cruz, siendo éste el límite sur de distribución del género. Habita en bordes de caminos, médanos, entre los 300 y 2800 m.

Observaciones. Moldenke (1962) cita la especie para Chile, sobre la base del ejemplar de Malleco: *Benh 9031* (S), el cual no se ha podido ubicar.

Material adicional examinado. ARGENTINA. **Chubut:** Dpto. Escalante, Pico de Salamanca, *Castellanos s.n. BA 6182* (SI); Dpto. Florentino Ameghino, a 7 km del cruce de ruta prov. 28 con ruta nac. 3, *Correa 10230* (CTES, SI); Dpto. Mártires, ruta nac. 25 a 52 km este de Las Plumas, *Arroyo 30* (SI); Dpto. Paso de los Indios, ruta nac. 25 a 62 km E de paso de Los Indios, *Arroyo 434* (CTES); Dpto.

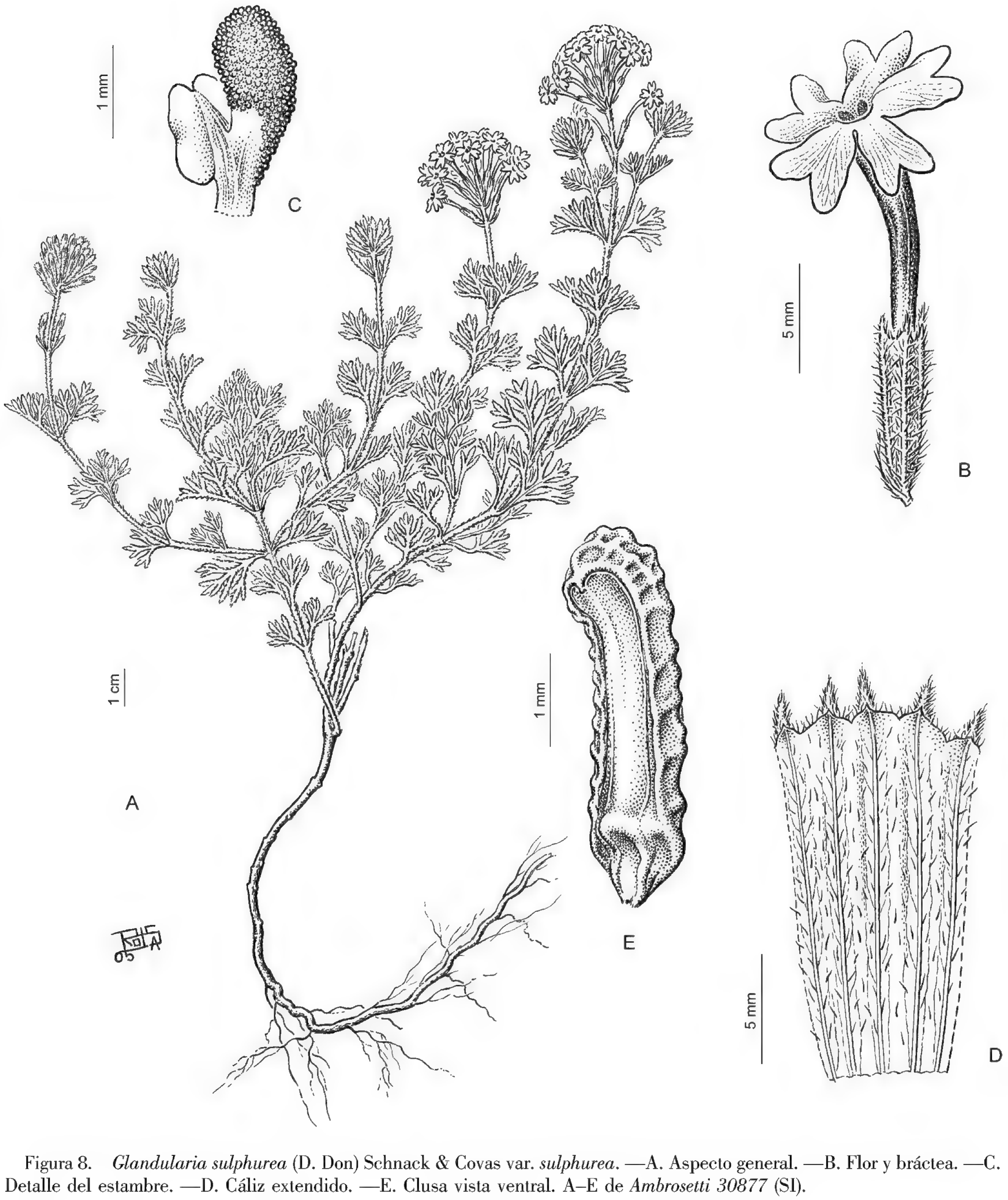

Figura 8. *Glandularia sulphurea* (D. Don) Schnack & Covas var. *sulphurea*. —A. Aspecto general. —B. Flor y bráctea. —C. Detalle del estambre. —D. Cáliz extendido. —E. Clusa vista ventral. A–E de *Ambrosetti 30877* (SI).

Rawson, ruta prov. 53, *Bonifacio 703* (SI); Dpto. Río Senguerr, Río Mayo, *Vallerini 3779* (SI); Dpto. Sarmiento, Colhue-Huapi, *Ameghino s.n. LP10005* (LP). **Mendoza:** Dpto. Las Heras, Cerros y Pampa de la Palcata, *Ruíz Leal 22009* (SI); Dpto. Malargüe, portezuelo del Choique, *Ruíz Leal 24324* (SI); Dpto. San Rafael, *Kurtz 5605* (SI); Dpto. Tupungato, ruta prov. 94, entre El Manzano y Portezuelo Argentino, ca. Arroyo Grande. Paraje Arroyo El Salto, *Cocucci 2244* (CTES, SI). **Neuquén:** Dpto. Aluminé, s. loc., *Asp 157* (BAF); Dpto. Catán Lil, a 6 km de Las Cortaderas hacia Carahuila, *Correa 7904* (CTES, SI). **Río Negro:** Dpto. Pilcaniyeu, Clemente Onelli, *s. coll. 5856* (SI). **Santa Cruz:** Dpto. Deseado, Próximo a Ea. Romberg, ruta prov. 12, en el cruce con el río Deseado, *Correa 10291* (SI).

5b. Glandularia aurantiaca var. **glabra** (Hicken) P. Peralta, comb. nov. Basiónimo: *Verbena radicata* Moldenke var. *glabra* (Hicken) Moldenke, Phytologia 9: 184. 1963. Nombre reemplazante para *Verbena radicans* Gillies & Hook. ex Hook. var. *glabra* Hicken, Darwiniana 1: 66. 1923,

nom. illeg. TIPO: Argentina. Mendoza: Arroyo Calabozo, dic. 1911, *Gerth, E. 32* (holotipo, SI 3731!). Figura 3.

Verbena aurantiaca Speg. var. *glaberrima* Moldenke, Phytologia 5: 341. 1956, syn. nov. *Glandularia aurantiaca* Speg. var. *glaberrima* (Moldenke) Botta, Parodiana 8: 31. 1993. TIPO: Argentina. Dpto. Malargüe: Alto Valle del Atuel, 2100 m, 9–17 ene. 1954, *A. Ruíz Leal & F. A. Roig 15723* (holotipo, NY no visto; isotipos, LL no visto, LL foto SI!, SI!).

Brácteas con margen ciliado, el resto de las superficies glabras; cáliz glabro o con muy pocos tricomas cortos y dispersos.

Distribución geográfica y hábitat. *Glandularia aurantiaca* var. *glabra* tiene una distribución restringida a las provincias de Mendoza y Neuquén. Crece entre los 1800 y los 2500 m.

Observaciones. En la descripción original de *Verbena radicans* var. *glabra* Hicken (1923: 66) dice: "... glandula antherarum abortiva, vix perspicua". Principalmente por esta característica se realiza la combinación de la variedad, bajo la especie *Glandularia aurantiaca*, ya que en *G. radicata* los apéndices conectivales están bien desarrollados.

Moldenke (1963a) crea el nombre *Verbena radicata* var. *glabra*, para reemplazar el nombre *V. radicans* var. *glabra* porque el epíteto específico "*radicans*" fue utilizado previamente por Moench (1794) bajo el mismo género, por lo tanto el nombre de Hicken pasa a ser un homónimo posterior.

En la descripción original de *Verbena flava* f. *abortiva* Hicken (1923: 66) dice: "*Glandulis antherarum* minutissimis, vix perspiculis...", luego Hicken aclara que las glándulas abortan. Esta descripción es similar a la anterior y prácticamente tienen la misma distribución geográfica, pero el tipo no fue ubicado.

Material adicional examinado. ARGENTINA. **Mendoza:** Dpto. Malargüe, Altiplanicie del Payén, entre Pata Mora y Coipo Lauquen, *Prina 1520* (CTES, SI); Dpto. San Rafael, ladera N, Cuchilla de la Tristeza, Vega del Toro, *Marquez 43* (SI); Dpto. Tunuyán, Puesto Gendarmería Alférez Portinari, Valle del Arroyo Grande, entre el Puesto y puente camino hacia el Cajón del Arenal, *Boelcke 10139* (SI). **Neuquén:** Dpto. Añelo, Sierra Auca Mahuida, *Fabris 868* (SI); Dpto. Chos-Malal, Cajón del Arroyo del Cruce, *Boelcke 11236* (SI).

6. Glandularia cabrerae (Moldenke) Botta, Bol. Soc. Argent. Bot. 26: 243. 1990. Basiónimo: *Verbena cabrerae* Moldenke, Phytologia 1: 478. 1940. TIPO: Argentina. Salta: Dpto. Orán, Quebrada del Río Caraparí, 15 jul. 1937, *A. L. Cabrera 4199* (holotipo, NY 00138248, NY foto SI!; isotipos, LP!, SI!, US no visto).

Hemicriptófito erecto de 50–60 cm alt., rizomatoso, con tallos ascendentes, algunos decumbentes, gráciles, pubescencia estrigosa; entrenudos de 3.5–5 cm. Hojas con pecíolo de 2–3 mm, lámina de 2–4.5 × 1.5–3.5 cm, 3- ó 5-partida, contorno triangular, ápice agudo, base atenuada, ambas superficies estrigosas, de consistencia cartácea. Inflorescencia en pleiobotrios heterotéticos paniculiforme, paracladios frondosos con ramificaciones de primer y segundo orden. Florescencias en espigas multifloras, densas, raquis alargado en la fructificación; entrenudo basal de 25 mm; brácteas de 3–4 mm, ovadas a angostamente ovadas, estrigosa con glándulas estipitadas, ápice agudo a algo aristado, margen ciliado. Flores con cáliz de 6.5–7 mm, estrigoso, con glándulas estipitadas, dientes de 1–1.5 mm, subulados; corola de 10–12 mm, externamente glabra, lila o violáceas, fauce pubescente; par superior de estambres con apéndices conectivales breves, inclusos, no superando las tecas; estilo de 6–7 mm. Clusas de 3–4 mm, rectas, ápice obtuso, base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa reticulada, superficie interna con escasas papilas.

Iconografía. Botta (1990: 244, fig. 1); Troncoso y Botta (1993: 108, fig. 48A–I), sub *Glandularia cabrerae*.

Distribución geográfica y hábitat. *Glandularia cabrerae* se encuentra en las provincias del norte argentino y en Bolivia. Crece sobre suelos arenosos, orillas de ríos y barrancas costeras y dunas, entre los 250 y 1200 m.

Observaciones. *Glandularia cabrerae* es una especie muy similar a *G. cheitmaniana* por la forma de las brácteas, pubescencia y división foliar, las dos taxa pueden diferenciarse por el tamaño de las clusas (menores a 2.5 mm en *G. cheitmaniana* vs. mayores a 3 mm en *G. cabrerae*) y el pecíolo (mayor a 3 mm vs. menor a 3 mm), la forma de los dientes del cáliz (caudados vs. subulados) y la pubescencia de la corola (escasamente pubescencia vs. glabra).

Material adicional examinado. ARGENTINA. **Jujuy:** Dpto. Doctor Manuel Belgrano, Zapla, *Burkart 30591* (SI); Dpto. Ledesma, Camino al Arroyo Cafetal, *Ahumada 8655* (CTES, SI); Dpto. San Pedro, Puente del Río San Francisco, ruta a Palma Sola, *Cabrera 27551* (SI); Dpto. Santa Bárbara, El Fuerte, alrededores, *Rotman 819* (SI); Dpto. Tumbaya, camino a Tiraxi, *Medinaceli s.n.* (BAF). **La Rioja:** Dpto. Gral. Belgrano, ruta nac. 38, entre Chamical y Chañar, a 22 km de la primera, Campo Exp. Las Vizcacheras (INTA), *Biurrum 5369* (SI). **Salta:** Dpto. Anta, Parque Nac. El Rey, Río Popayán, 10 km al E de la hostería, *Novara 5673* (SI); Dpto. Chicoana, Serranías a W de ruta nac. 68, Km 138, siguiendo por ruta prov. 32, Km 4, entre Viñaco y Chicoana, 4–5 km al S de Chicoana, *Tolaba 2312* (CTES); Dpto. Gral.

José de San Martín, Sierra del Alto, Río Seco a 40 km de Cnel. Cornejo, después de Arroyo Seco, *Cabrera 34464* (SI); Dpto. Orán, Caraparí, *Maldonado 833* (SI). BOLIVIA. **Chuquisaca:** Luis Calvo, El Salvador, Laguna Seca, Campo Quemado, *Pensiero 4381* (SI). **Santa Cruz de la Sierra:** Sara, W side of Rio Pirai, 0.5 km downstream and N of the Eisenhower bridge of the hwy. from Montero to Portachuelo, 7 km ENE of Portachuelo and 8 km W of Montero, *Nee 39732* (SI). **Tarija:** O'Connor, abra de la cuesta de San Simón, *Krapovickas 39050* (CTES).

7. Glandularia cheitmaniana (Moldenke) Botta & Poggio, Parodiana 5: 333. 1988. Basiónimo: *Verbena cheitmaniana* Moldenke, Phytologia 2: 420. 1948. TIPO: Argentina. Jujuy: El Piquete, Río San Francisco, 21 ago. 1901, *R. E. Fries 477* (holotipo, S no visto, S foto SI!; isotipos, NY 00138253!, SI!).

Hemicriptófito erecto de 20–50 cm alt., apoyante formando matas o manchones de hasta 1 m de diámetro, escasamente híspida, de ramas floríferas ascendentes, radicante en nudos basales; entrenudos de 2–7 cm. Hojas con pecíolo de 3–8 mm, lámina de 1.5–6.5 × 1–3.5 cm, membranáceas, contorno triangular-ovado, 3-partidas, ápice agudo, estrigosa en ambas superficies. Inflorescencias en monobotrios o pleiobotrios con 1 ó 2 pares de paracladios frondosos o no. Florescencias en espigas densas, multifloras, raquis alargado en la fructificación; entrenudo basal de 10–40 mm; brácteas de 3–4 mm, angostamente ovadas, ápice atenuado a aristado, superficie abaxial estrigosa, margen ciliado. Flores con cáliz de 6.5–7.5 mm, pubescencia híspida a estrigosa, escasas glándulas pateliformes, dientes de 1–2 mm, caudados; corola de 9–12 mm, violeta, escasa pubescencia externa, fauce pubescente, lóbulos escotados; par superior de estambres con apéndices conectivales breves, inclusos menores a la longitud de las tecas; estilo de 6.5 mm. Clusas de 2–2.5 m, algo curvas, ápice obtuso, base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa reticulada hacia el ápice, interna lisa o con escasas papilosa.

Iconografía. Troncoso y Botta (1993: 108, fig. 48 J–P); Botta y Poggio (1988: 334, fig. 1), sub *Glandularia cheitmaniana*.

Distribución geográfica y hábitat. Glandularia cheitmaniana crece en las provincias del norte de la Argentina, entre los 500 y 2600 m, sobre bordes de caminos y lechos secos de ríos.

Observaciones. Glandularia cheitmaniana es una especie similar a *G. cabrerae*, ver observaciones de la especie anterior.

Material adicional examinado. ARGENTINA. **Chaco:** Dpto. Almte. Brown, Pampa de los Guanacos, *Spegazzini 10559* (BAF). **Jujuy:** Dpto. Doctor Manuel Belgrano, Sierra de Zapla, camino a la mina 9 de Octubre, Antena, *Zuloaga 7625* (SI); Dpto. Ledesma, Toma del río Zora, *Ahumada 5212* (CTES, SI); Dpto. San Pedro, camino de San Pedro a Ledesma, a 10 km de San Pedro, El Quemado, *Botta 332* (SI); Dpto. Santa Bárbara, NE of Ldor., ca. 11–12 km by rd. S of Palma Sola on rd. to El Sauzal, *Taylor 11459* (SI). **Salta:** Dpto. Anta, Parque Nac. El Rey, *Novara 506* (SI); Dpto. Cafayate, ruta nac. 68, 86 km N Cafayate, *Cordo s.n.* (SI); Dpto. Chicoana, Chicoana, *Martínez Crovetto 6088* (SI); Dpto. Gral. Güemes, Gral. Güemes, *Holmberg s.n. 10467* (SI); Dpto. La Viña, Cnel. Moldes, La Hoyada, *Burkart 13202* (SI); Dpto. Metán, El Galpón, *Martínez Crovetto 3378* (SI); Dpto. Orán, río Piedras, *Rodríguez 19* (BAF); Dpto. Rosario de la Frontera, ruta nac. 9, de Rosario de la Frontera a San Miguel de Tucumán, *Cialdella 572* (CTES, SI); Dpto. Santa Victoria, alrededores de Santa Victoria, *Kiesling 3968* (SI). **Tucumán:** Dpto. Tafí, Tafí del Valle, *Venturi 2898* (SI). BOLIVIA. **Santa Cruz de la Sierra:** a 10 km entre Palmasola y Lomas de Arena, *Hunziker, J. H. 13071* (SI).

8. Glandularia dissecta (Willd. ex Spreng.) Schnack & Covas, Darwiniana 6: 475. 1944. Basiónimo: *Verbena dissecta* Willd. ex Spreng., Syst. Veg. (ed. 16) [Sprengel] 2: 750. 1825. *Shuttleworthia dissecta* (Willd. ex Spreng.) Walp., Repert. Bot. Syst. [Walpers] 4: 12. 1845. TIPO: Chile. "Montevideo (Uruguay), o Buenos Aires (Argentina)", s.d., *L. Nee s.n.* (holotipo, B-W 11139 no visto, B foto F 17460 en NY!, B foto F 17460 en SI!).

Verbena dissecta Willd. ex Spreng. f. *capitata* Moldenke, Phytologia 52: 330. 1983. TIPO: Uruguay. Montevideo: Pajas Blancas, 5 oct. 1935, *W. G. Herter 1805* (holotipo, US no visto, US foto SI!).

Verbena pulchella Sweet f. *latilobata* Moldenke, Phytologia 3: 281. 1950, syn. nov. TIPO: Uruguay. Montevideo: Barra Santa Lucía, 30 oct. 1907, *M. B. Berro 4751* (holotipo, NY 00138311!, NY foto SI!; isotipos, SI 3801!).

Hemicriptófito rastrero hasta de 50 cm de altura, perenne, tallos rastreros, radicantes en la base, híspidos; entrenudos de 1.5–4.5 cm. Hojas con pecíolo de 0.3–1 cm, lámina de 1.2–3.5 × 1–3 cm, contorno triangular-oval, 3- ó 5-partidas a 3-sectas, bipinnatipartidas, lóbulos lineares a angostamente ovados ápice obtuso, margen revoluto; cara adaxial hirsuta, cara abaxial con tricomas rígidos y densos sobre los nervios y márgenes. Inflorescencia en pleiobotrios heterotéticos, 1 a 3 pares de paracladios, los más distales frondosos, sobrepasando o no la florescencia principal. Florescencia en espigas densas, raquis no alargado en la fructificación; entrenudo basal de 10–25 mm; brácteas de 2.5–3 mm, lineares a angostamente ovadas. Flores del cáliz de 7–7.5 mm, hirsuto, pudiendo presentar glándulas

casi sésiles sobre las costillas, dientes hasta de 1 mm; corola de 9–11 mm, violácea, pubescente exteriormente en la parte superior, fauce pubescente; par superior de estambres con apéndices conectivales mayores que las tecas, exertos; estilo de 7 mm. Clusas de 2–2.5 mm, curvas, algo arriñonadas, ápice redondeado, base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa marcadamente reticulada, superficie interna lisa.

Iconografía. Troncoso (1939: 483, fig. 2), sub *Glandularia dissecta*.

Distribución geográfica y hábitat. Glandularia dissecta crece en Argentina en la provincia de Buenos Aires, Uruguay en los departamentos de San José y Montevideo, sobre suelo arenoso.

Observaciones. En la etiqueta del ejemplar tipo de *Verbena dissecta* se lee "Chile" como lugar de colección, lo cual corresponde a un error geográfico, ya que L. Neé, tripulante de la Expedición Malaspina, recorre las costas del Río de La Plata, y es muy probable que dicho material provenga de Montevideo (Uruguay), o de Buenos Aires (Argentina). Dicho argumento se fundamenta además, en que el material adicional estudiado es de procedencia Rioplatense (Buenos Aires y costas del Uruguay). El material estudiado procedente de Chile y determinado en un principio como *V. dissecta* corresponde a otras especies exclusivas de Chile.

Se considera sinónimo a *Verbena pulchella* f. *latilobata*, porque al mirar el material tipo pudo comprobarse que las características observadas no difieren de los caracteres de *Glandularia dissecta*.

Glandularia dissecta es similar a *G. tenera* por el hábito y la división foliar; la última se diferencia por presentar las inflorescencias en espigas más densas y no alargada en la fructificación, y por las glándulas anterales de mayor tamaño y netamente visibles en la garganta del tubo corolar.

Material adicional examinado. ARGENTINA. **Buenos Aires:** Pdo. Balcarce, Sierra Volcán, *Hunziker 8330* (LP); Pdo. Campana, *Troncoso 172* (SI); Pdo. Gral. Pueyrredón, Ojo de Agua, cerros, *Cabrera 10352* (LP); Pdo. La Plata, Los Talas, *Alboff s.n. LP 8345* (LP); Pdo. Lobería, *Spegazzini s.n.* (LP); Pdo. Magdalena, ruta nac. 11, entre Magdalena y Punta de Indio, *Fabris 6636* (CTES, LP); Pdo. San Isidro, s. loc., *Troncoso s.n. SI 27689* (SI); Pdo. Zárate, Las Palmas, *Boelcke 4923* (SI). URUGUAY. **Colonia:** Río San Juan, dunas, *Cabrera 3226* (LP). **Montevideo:** Pajas Blancas, *Herter 1805* (SI). **San José:** Rincón del Pino, *Izaguirre 9584* (SI).

9. Glandularia flava (Gillies & Hook. ex Hook.) Schnack & Covas, Darwiniana 6: 475. 1944.

Basiónimo: *Verbena flava* Gillies & Hook. ex Hook., Bot. Misc. 1: 170. 1830. TIPO: Argentina. Mendoza: "In collibus prope Rio del Diamante", *C. B. Gillies s.n.*, p.p. [a la derecha] (lectotipo, aquí designado, K 000470720!; isotipos, E 00259075!, E 00259076!, E 00259077!, K foto SI!).

Verbena glutinosa Kuntze, Revis. Gen. Plant. 3(2): 256. 1898, syn. nov. *Glandularia glutinosa* (Kuntze) Covas & Schnack, Darwiniana 7: 72. 1945. TIPO: Argentina. Paso Cruz, 34°, 1500 m, June 1892, *O. Kuntze s.n.* (holotipo, NY 00138268!, NY foto SI!; isotipos, SI!, US 00118694 no visto, US 118693 no visto, US foto SI!, W no visto).

Verbena flava Gillies & Hook. ex Hook. var. *angustiloba* Speg., Anales Soc. Ci. Argent. 53: 249. 1902. TIPO: Argentina. "in aridis secus Río Negro, loco El Carbón vocato prope Carmen de Patagones", feb. 1898, *C. Spegazzini s.n.* (holotipo, LP 13522!).

Verbena flava Gillies & Hook. ex Hook. var. *latiloba* Speg., Anales Soc. Ci. Argent. 53: 249. 1902. TIPO: Valle del Río Chubut, 5 dic. 1898, *V. R. 59* [?] (holotipo, LP 13519!).

Sufrútice de 30–50 cm, postrado. Ramas glabras; entrenudos de 1–2 cm. Hojas sésiles, lámina de 1.5–4(–5) × (1–)2.5–6(–7) cm, linear a ovado-elípticas, enteras, a veces irregularmente partidas, ápice agudo, superficies glabras, margen entero. Inflorescencia en monobotrios o pleiobotrio heterotéticos paniculiformes con 2 pares de paracladios muy desarrollados que vuelven a dividirse siguiendo un mismo patrón. Florescencias en espigas terminales densas, multifloras, umbeliformes, raquis algo alargado en la fructificación; entrenudo basal de 2.5–5 cm; brácteas de 2–2.5 × ca. 1 mm, ovadas, glabras, ciliadas en el margen, vena media bien marcada. Flores con cáliz de 9–12 mm, estrigoso con escasos tricomas glandulares, de densidad variable, dientes subiguales; corola de 13–16 mm, amarillo pálido, cremoso, glabra en la superficie externa, fauce pubescente; par superior de estambres con apéndices conectivales, de longitud variable, exertos, pardos; estilo de 13–14 mm. Cáliz fructífero contorto en el ápice; clusas de 5–5.5 mm, pardos, ápice rostrado, apículo de longitud variable, base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa reticulada, superficie interna con papilas escasas.

Iconografía. Botta (1993: 32, fig. 9), sub *Glandularia flava*.

Nombre vulgar. Pasto de oveja, ejemplar *A. Petrocelli 36* (SI).

Distribución geográfica y hábitat. Glandularia flava se encuentra ampliamente distribuida en

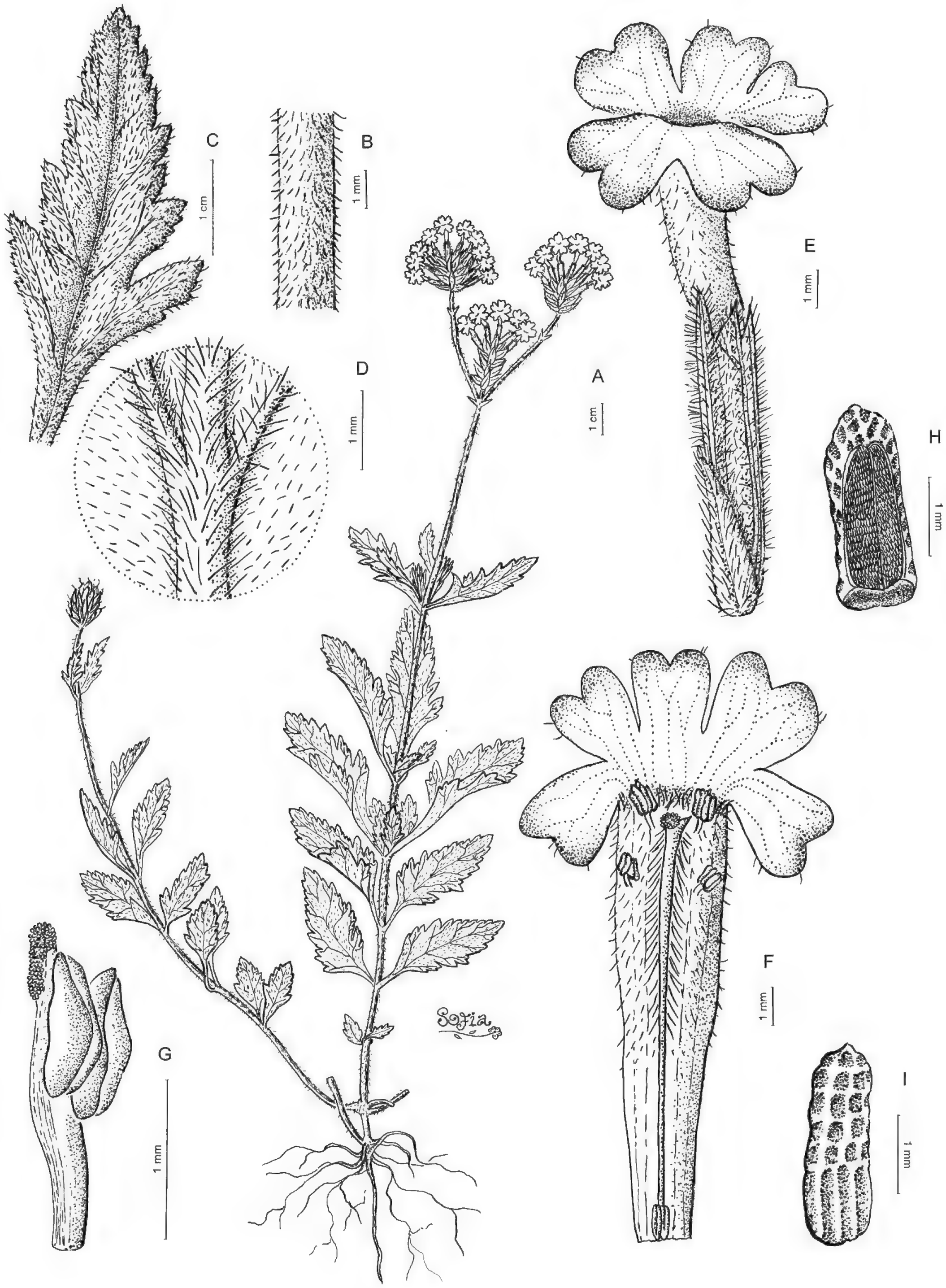

Figura 9. *Glandularia tomophylla* (Briq.) P. Peralta. —A. Aspecto general. —B. Detalle de la pubescencia del tallo. —C. Hoja, superficie adaxial. —D. Detalle de la hoja, superficie abaxial. —E. Flor y bráctea. —F. Corola expandida mostrando la pubescencia y la inserción de los estambres y gineceo. —G. Detalle de los estambres. —H. Clusa, vista ventral. —I. Clusa, vista dorsal. A–I de *Rojas 11785* (SI).

Argentina desde la provincia de La Rioja hasta Chubut en el sur, entre los 120 y 2000 m, sobre suelos arenosos y pedregosos.

Observaciones. Hooker al describir *Verbena flava*, nombra en el protólogo (1830: 170): "In convallibus Andinum Mendozam versus, et in collibus prope Rio del Diamante...", se han encontrado dos ejemplares coleccionados por Gillies, uno depositado en el herbario HAR, el cual sólo dice: "Mendoza", y el otro depositado en K (Hb. Hookerianum) también de Mendoza, Río Diamante. Se elige como lectotipo los materiales ubicados a la derecha y hacia arriba de la cartulina del último ejemplar anteriormente citado, por corresponderse exactamente con el protólogo. El resto de material, ubicado a la izquierda y debajo de la cartulina podrían corresponderse a *Glandularia aurantiaca*.

Glandularia flava es afín a *G. aurantiaca* y *G. araucana* por ser sufrútices glabrescentes, presencia de apéndices glandulares y coloración de la corola; se diferencian porque las últimas presentan las clusas con ápice obtuso, hojas pecioladas y la división foliar.

Material adicional examinado. ARGENTINA. **Buenos Aires:** Pdo. Villarino, Médanos, ruta nac. 3, Km 735, *Seijo 1425* (CTES). **Chubut:** Dpto. Biedma, Península de Valdez, Puerto Pirámides, *Villamil 2725* (SI); Dpto. Escalante, Puerto Pirámides, *Cabrera 21205* (LP). **La Pampa:** Dpto. Chalileo, 24 km E de Santa Isabel, *Hunziker 8312* (SI); Dpto. Chical-Có, Agua de Torres, *Adler 30* (SI); Dpto. Puelen, Barda Baja, *Cano 800* (SI). **La Rioja:** Sin dpto., Alto Blanco, Balde de San Herrera, *Frenguelli s.n. LP 894645* (LP). **Mendoza:** Dpto. Gral. Alvear, ruta prov. 188, entre Los Huarpes y La Mora, *Cano 2559* (CTES); Dpto. La Paz, entre Maquinista Levet y Río Tunuyán, *Ruíz Leal 8960* (SI); Dpto. Las Heras, Ramblon, *Ruíz Leal 9291* (SI); Dpto. Malargüe, El Sosneado, *Schnack 21* (SI); Dpto. San Rafael, Patimalal, *Ruíz Leal 7500* (SI). **Neuquén:** Dpto. Aluminé, Río Aluminé, ruta nac. 40, *Schajovskoy 49/III, SI 25627* (SI); Dpto. Añelo, Sierra Auca Mahuida, *Fabris 842* (LP, SI); Dpto. Catán Lil, 8 km al S de Las Coloradas, *Cabrera 32992* (SI); Dpto. Chos-Malal, borde del río Neuquén, frente al cerro de la Virgen, *Ancibor s.n. BAB 90186* (BAB, SI); Dpto. Confluencia, Colonia Centenario, N de la Patagonia, *Rasp 177* (SI); Dpto. Los Lagos, entre Neuquén y Bariloche, *Offermam s.n.* (SI); Dpto. Minas, a 5 km de Las Ovejas, camino a las lagunas Epu-Lauquen, subida a Mallín Verde, *Boelcke 10774* (SI); Dpto. Picún Leufú, en las colonias áridas y pedregosas de la márgen derecha, a la altura del puente sobre ruta 40, *Ruíz Leal 26853* (SI); Dpto. Picunches, Colunco, *Ammann 111* (SI); Dpto. Zapala, La Negra, a 100 km de Zapala, *Ruíz Leal 24337* (SI). **Río Negro:** Dpto. 9 de Julio, Laguna Azul, en la meseta de Somuncurá, *Troiani 15121* (CTES, SI); Dpto. Adolfo Alsina, 73 km S de Viedma, *Correa 6810* (CTES, SI); Dpto. Avellaneda, Isla Choele Choel, *Ruíz Leal 25505* (SI); Dpto. Conesa, 31 km al S, *Correa 3180* (SI); Dpto. El Cuy, de cerro Policía a Trica-co, *Cabrera 18658* (CONC, CTES, LP, SI); Dpto. Gral. Roca, J. J. Gómez, orillas del río Negro, *Krapovickas 22425* (CONC, CTES, SI); Dpto. San Antonio: Las Grutas, *Villamil 3232* (SI); Dpto. Valcheta, De Valcheta a Somuncurá, *Ruíz Leal 26196* (SI). **San Juan:** Dpto. Caucete, ruta nac. 141, médanos de las afueras de Caucete, *Biurrum 6202* (CTES, SI); Dpto. Jáchal, ruta 40, a 62 km de San Juan, *Delucchi 2511* (LP). **San Luis:** Dpto. Gdor. Dupuy, entre Nueva Galia y Arizona, *Guiñazú p.p. 226* (SI).

10. Glandularia guaranitica Tronc., Darwiniana 16: 618–621, fig. 3. 1971. *Verbena guaranitica* (Tronc.) Moldenke, Phytologia 23: 211. 1972. TIPO: Argentina. Corrientes: Dpto. San Martín, Tres Cerros, 8 Nov. 1936, *A. Burkart 8028* (holotipo, SI 3803!; isotipo, SI 3804!).

Sufrútice de 50–120 cm alt., radicante, ascendente, ramas apoyantes, pubescencia híspido-glandulosa, entrenudos de 5–8 cm, tallo cuadrangular. Hojas con pecíolo de 5–15 mm, lámina de 3–10 × 0.9–2.7 cm, enteras, ovadas a subtriangulares, ápice agudo, base cuneada, margen irregularmente serrado, cara adaxial estrigosa, cara abaxial híspida fundamentalmente sobre las venas a veces con escasos tricomas glandulares. Inflorescencia en pleiobotrios heterotéticos, con 1 ó 2 pares de paracladios bracteosos que sobrepasan o no a la florescencia principal. Florescencias en espigas densas multifloras, raquis no alargado en la fructificación; entrenudo basal de 7–25 mm; brácteas basales de 1.5–2 mm, ovales; superiores de 2–3 mm, ovales a angostamente ovales, pubescencia híspida a estrigosa sobre la superficie, margen ciliado con tricomas más largos. Flores con cáliz de 11–14 mm, densamente híspido, con algunos tricomas glandulares, dientes de 1–1.2 mm, subiguales, agudos, triangulares; corola de 19–25 mm, violácea mitad superior con breves tricomas glandulares, resto glabra, fauce pubescente, lóbulos subiguales, escotados; par superior de estambres con apéndices conectivales reducidos, sésiles en la base del conectivo; estilo de 19–20 mm. Clusas de 6 mm, ápice rostrado, base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa reticulada, superficie interna papilosa.

Iconografía. Troncoso (1971: 619, fig. 3), sub *Glandularia guaranitica*.

Nombre vulgar. Margarita, en los ejemplares *J. E. Montes 1747* (LP, SI), *2521* (LP), *12609* (CTES, LP).

Distribución geográfica y hábitat. Glandularia guaranitica habita en el este de Argentina, sur de Brasil y Paraguay. Crece sobre terrenos altos a orillas de bosques, hasta los 300 m.

Observaciones. Glandularia guaranitica es una especie similar a *G. phlogiflora* y *G. megapotamica*

por las hojas enteras, el no alargamiento del raquis en la fructificación, ápice de las clusas y los apéndices conectivales sin desarrollo de pie; *G. phlogiflora* se deferencia de *G. guaranitica* por la pubescencia hirsuto-escabosa del tallo, el mayor tamaño de las brácteas florales y los dientes de cáliz subulados; mientras que *G. megapotamica* se diferencia por presentar tallos, hojas y cálices ralamente estrigosos. También suele ser confundida con *G. peruviana* y *G. tweedieana*, especies que se diferencian porque la inflorescencia se alarga notablemente después de la antesis, por la ausencia de glándulas conectivales y por tener flores rojas.

Material adicional examinado. ARGENTINA. **Buenos Aires:** Pdo. Ensenada, Punta Lara, *Fabris 3191* (LP). **Corrientes:** Dpto. Concepción, Ea. El Fortín del Iberá, *Pedersen 9078* (SI); Dpto. Gral. Paz, Estero Malo, ruta nac. 5, 17 km E de Caá-Catí, *Carnevalli 4260* (CTES); Dpto. Ituzaingó, Ea. San Pedro, *Arbo 1113* (CTES); Dpto. San Cosme, 2 km E de Santa Ana, *Schinini 13002* (SI); Dpto. San Martín, Río Aguapey y ruta nac. 40, *Tressens 4112* (CTES); Dpto. San Miguel, ruta nac. 12, Km 1100, *Carnevali 2621* (CTES); Dpto. Santo Tomé, Ea. Francisco, 23 km NW de Gdor. Virasoro, *Krapovickas 17226* (SI). **Entre Ríos:** Sin dpto., Delta del Paraná, río Ceibo, *Cabrera 1962* (LP). **Misiones:** Dpto. Apóstoles, Escuela Agrotéc. P. Gentilini, *Cabrera 28744* (SI); Dpto. Cainguás, Predio UNLP, Reserva Valle del Arroyo Cuña Pirú, Picada desde la Est. Biol. hasta el arroyo Liso, *Biganzoli 1465* (SI); Dpto. Candelaria, pasando el puente de Santa Ana, rumbo hacia el río, *Barboza 422* (CTES, SI); Dpto. Capital, Posadas, *Alboff s.n. LP 8498* (LP); Dpto. Leandro N. Alem, ca. 2 km N of Cerro Azul on ruta prov. 3, *Olmstead 2004-124* (SI); Dpto. Ldor. Gral. San Martín, Predio UNLP, valle del Arroyo Cuña Pirú, camino abandonado entre el Balneario y la ruta 7, *Biganzoli 118* (LP, SI); Dpto. Oberá, ruta 105 a 23 km al W de Oberá, *Romanczuk 718* (SI); Dpto. San Ignacio, Jardín América, *Vanni 3856* (CTES). BRASIL. **Rio Grande do Sul:** Pelotas, Morro Redondo, *Pedersen 12592* (CTES, SI). **Santa Catarina:** São Joaquim, banks of Rio Taimbezinho, 1 km E of Bom Jardim da Serra (Cambajuva), *Smith 10203* (SI). PARAGUAY. **Alto Paraná:** in regione fluminis Alto Paraná, *Fiebrig 6452* (SI). **Caaguazú:** 10 km N de Caaguazú, camino a Yhú, *Krapovickas 12550* (CTES, SI). **Central:** Estero del Ypoá, 2 km W of Pindoty, *Zardini 23186* (SI). **Guairá:** Colonia Independencia, región de Villa Rica, *Rojas 4736* (SI). **Itapúa:** Isla Yaciretá, *Pin 333* (CTES). **Misiones:** 10 km N de Ayolas, *Schinini 25980* (CTES). **Paraguarí:** Ybytirú, *Montes 12989* (LP).

11. Glandularia hassleriana (Briq.) Tronc., Darwiniana 19: 738. 1975. Basiónimo: *Verbena hassleriana* Briq., Bull. Herb. Boissier, ser. 2, 4: 1056. 1904, como "*hasslerana*". TIPO: Paraguay. [Cordillera?]: "prope Tobaty in palude", Set., *E. Hassler 6464* (lectotipo, aquí designado, G no visto, G foto SI!; isotipos, K no visto, K foto SI!, MO no visto, MO foto SI!, NY 0138270!, NY foto SI!, P no visto, S no visto, S foto SI!, SI 3791!, US no visto, US foto SI!). Figura 4.

Sufrútice de hasta 1 m de alt., tallo cuadrangular híspido, entrenudos de 6–10 cm. Hojas con pecíolo de 0.8–2.5 cm, lámina de 3–10 × 0.7–3.5 cm, elíptica a ovada, enteras, ápice agudo, base atenuada, margen serrado, ambas superficies estrigosas. Inflorescencia en pleiobotrios heterotéticos o monobotrios. Florescencia en espigas densas multifloras, raquis alargado en la fructificación; entrenudo basal de 2.5–5 cm; brácteas de 9–10.5 mm, angostamente ovadas, ciliadas, estrigosas híspida sobre la vena media. Flores con cáliz de 10–11 mm, híspido, sobre las costillas, resto glabro, dientes de 3–4 mm; corola de 18 mm, rosada, violeta o lila, externamente glandulosa, fauce pubescente; par superior de estambres con apéndices conectivales, menores que las tecas, sin pie, inclusos en la corola; estilo de 17 mm. Clusas de 4–5 mm, ápice rostrado, base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa reticulada hacia el ápice, acanaladas hacia la base, superficie interna papilosa.

Nombre vulgar. Yerba de la china, margarita amarga, flor de vovia (Moldenke & Moldenke, 1949).

Distribución geográfica y hábitat. Glandularia hassleriana crece en el noreste de Argentina, y en el sur de Brasil, Paraguay y Uruguay. Habita sobre campos pantanosos, arenosos y húmedos, suelos pedregosos, hasta los 300 m.

Observaciones. Briquet (1904b) cita en el protólogo tres sintipos (*Hassler 3550*, *Hassler 6401*, *Hassler 6464*), se elige como lectotipo el ejemplar de *Hassler 6464*, porque coincide con el protólogo de la especie. Briquet en la descripción original (1904b: 1056), describe la inflorescencia como: ". . .Flores in spicas abbreviatas terminales...", carácter que no se corresponde con los ejemplares tipo vistos, en ellos puede apreciarse claramente el alargamiento del raquis en la fructificación. Briquet (1904b), agrega a la sinonimia de esta especie a *Verbena phlogiflora* Chod., el cual es un nombre inexistente.

Glandularia hassleriana es una especie similar a *G. nana* por la morfología foliar, ápice de las clusas y par superior de estambres; esta última se diferencia por el tamaño de las clusas (ca. 6 mm vs. 4–5 mm en *G. hassleriana*), brácteas de menor tamaño (ca. 4 mm vs. ca. 10.5 mm) y la pubescencia de los tallos hirsuta-glandulosa (vs. híspido).

Material adicional examinado. ARGENTINA. **Corrientes:** Dpto. Ituzaingó, 11 km N de San Carlos, *Krapovickas 24989* (CTES); Dpto. Mburucuyá, Ea. Santa Teresa, *Cabrera 28190* (SI); Dpto. San Roque, Ea. Caaguazú, 11 km NE de Chavarría camino a Tacuaritas, potrero Plantel, aprox. 3 km al W del casco, *Arbo 6873* (CTES); Dpto. Santo Tomé, Garruchos, *Krapovickas 21608* (SI). **Misiones:** Dpto.

Apóstoles, ruta nac. 14, 10 km al N de San José, *Guaglianone 903* (SI); Dpto. Candelaria, Loreto, *Schinini 27597* (CTES, SI); Dpto. San Ignacio, entre San Ignacio y Santa Ana, ruta nac. 12, 86 km da fronteira com Corrientes, *Forzza 1941* (SI). BRASIL. **Rio Grande do Sul:** Gr. Piratini Santo Ángelo, *Hagelund 8139* (SI). **Santa Catarina:** 10 km E de Ponte Serrada, *Krapovickas 33701* (CTES). PARAGUAY. **Alto Paraguay:** Chaco, Puerto Casado, *Rojas 1895* (SI). **Caaguazú:** 8 km N of Caaguazú on the rd. to Yhú, *Harley 28039* (CTES). **Guairá:** Colonia Independencia, *Schinini 25241* (CTES). **Misiones:** Tajuyí-hý near San Ignacio, *Pedersen 5234* (SI). **Paraguarí:** Ybitimi, *Montes 12961* (CTES). **Presidente Hayes:** betw. Pozo Colorado & Concepción, *Zardini 58679* (SI). URUGUAY. **Rivera:** R 5, al N de Tranqueras, *Rosengurtt B-8042* (SI).

12. Glandularia lilloana (Moldenke) Botta, Bol. Soc. Argent. Bot. 29: 244. 1990. Basiónimo: *Verbena lilloana* Moldenke, Phytologia 3: 176. 1949. TIPO: Argentina. Tucumán: Dpto. Chicligasta, Las Pavas, 3000 m, 22 nov. 1926, *S. Venturi 4607* (holotipo, NY 00138282!, NY foto SI!; isotipos, CAS 004919!, LIL 001374!, LIL 001373!, SI 003785!, UC 0342572!, US 00118710!, US foto SI!).

Hemicriptófito de 40–60(–80) cm alt., rastrera o apoyante, tallos ascendentes, escasamente estrigosos, radicante en los nudos basales; entrenudos de 6–10(–15) cm. Hojas con pecíolos de 1–1.5 cm, lámina de 3–6 × 2–3.5 mm, contorno triangular, 3-partidas a 3-sectas, generalmente los lóbulos de margen inciso-lobado, membranácea, ambas superficies escasamente estrigosas, algo híspidas sobre las venas. Inflorescencia en pleiobotrios, con 1 ó 2 pares de paracladios bracteosos, no ramificados, que sobrepasan o no la florescencia principal. Florescencias en espigas densas, multifloras, raquis alargado en la fructificación; entrenudo basal de 5–13 cm; brácteas de 5–6.5 mm, anchamente ovadas, escasamente pubescentes, de ápice agudo a aristado, el margen algo membranáceo. Flores con cáliz de 6–8 mm, híspido a estrigoso, dientes hasta 1 mm, aristados; corola de 10–14 mm, externamente pubescente o no, fauce pubescente, tubo internamente piloso; lóbulos escotados; par superior de estambres con apéndices conectivales no sobrepasando las tecas o sólo apenas, inclusos; estilo de 8.5 mm. Clusas de 2.5 mm, curvas, ápice obtuso, base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa reticulada, superficie interna lisa.

Iconografía. Botta (1990: 245, fig. 2A–G); Troncoso y Botta (1993: 112, fig. 50A–G), sub *Glandularia lilloana*.

Distribución geográfica y hábitat. Glandularia lilloana se distribuye al norte y oeste de la Argentina. Es común en bordes de caminos, suelos pedregosos y laderas, entre los 900 y los 3200 m.

Observaciones. Glandularia lilloana es una especie similar a *G. cabrerae* y *G. cheitmaniana*, por el hábito, morfología foliar, pubescencia; las dos últimas especies se diferencian por presentar las brácteas anchamente ovadas menores a 5 mm de largo y las clusas rectas.

Material adicional examinado. ARGENTINA. **Catamarca:** Dpto. Andalgalá, ruta prov. 365, Cuesta del Clavillo, *Cocucci 2632* (SI); Dpto. El Alto, pasando Guayamba, Tintigasta, *Sayago 2683* (SI). **Jujuy:** Dpto. Doctor Manuel Belgrano, camino a Tiraxi, *Zuloaga 9108* (SI); Dpto. Gral. San Martín, entre Arroyo Aguas Negras y Calilegua, *Hunziker 12742* (SI); Dpto. Humahuaca, Sierra de Zenta, *Venturi 8356* (SI); Dpto. Ledesma, entre Río de Aguas Negras y Calilegua, *Hunziker 12742* (SI); Dpto. Santa Bárbara, Tierras de Maíz Gordo, 4 km del Infiernillo camino al Puerto de Maíz Gordo, próximo al Río Maíz Gordo, *Morrone 3032* (SI); Dpto. Tumbaya, Volcán, Chilcayo, camino a Abra Morada, *Kiesling 5767* (SI); Dpto. Tilcara, s. loc., *Petersen 57* (SI); Dpto. Valle Grande, 23 km del pueblo (al S), *Hunziker 12778* (SI). **Salta:** Dpto. Anta, Parque Nac. Finca El Rey, río Papoyán, *Correa 4284* (SI); Dpto. Orán, Aguas Blancas, ca. campamento, *Iudica 186* (SI). **Tucumán:** Dpto. Chicligasta, Cuesta del Clavillo, *Kiesling 1224* (SI); Dpto. Tafí, Cerro San José, *Venturi 3568* (SI).

13. Glandularia macrosperma (Speg.) Tronc., Darwiniana 19: 738. 1975. Basiónimo: *Verbena macrosperma* Speg., Revista Argent. Bot. 1: 218. 1926. TIPO: Argentina. Chubut: Sierra de Talagapa, ene. 1926, *A. Raffaelli s.n.* (holotipo, BAF!).

Verbena sulphurea D. Don var. *intermedia* Kuntze, Revis. Gen. Pl. 3(2): 258. 1898, syn. nov. *Glandularia sulphurea* (D. Don) Schnack & Covas var. *intermedia* (Kuntze) L. E. Navas, Flora de la Cuenca de Santiago de Chile 3: 69. 1979. TIPO: Argentina. Patagonia, abr. 1882, *F. J. P. Moreno y Tonini 330* (holotipo, NY 00138331 no visto, NY foto SI!; isotipo, SI!).

Sufrútice de 15–20 cm alt., rastrera, rizomatosa, base leñosa, muy ramificada; ramas híspidas, las floríferas erectas; entrenudos de 1.5–2 cm. Hojas con pecíolo de 2–4 mm, lámina de 1.2–1.5 × 0.6–1 cm, contorno oval-triangular, 3-sectas, bipinnatipartidas, superficies densamente híspidas; segmentos oblongos a elípticos, ápice obtuso, margen algo revoluto. Inflorescencia en pleiobotrios con 1 o más pares de paracladios a veces frondosos, ramificados o no. Florescencias en espigas densas multifloras, raquis algo alargado en la fructificación; entrenudo basal de 10–20 mm; brácteas basales de 3–4.5 mm, apicales de 1.5–2 mm, angostamente ovadas, ápice agudo, híspidas, margen ciliado. Flores con cáliz 7–10 mm, híspido a adpreso hacia la base, dientes abaxiales ca. 1 mm; corola de 12–22 mm, glabra exteriormente,

amarillenta, rosada, fauce pubescente; par superior de estambres con apéndices conectivales muy reducidos, inclusos, no superando las tecas; estilo de 10–19 mm. Clusas 5–6 mm, ápice obtuso, base no angostada y con repliegue basal y transversal de la pared comisural.

Iconografía. Botta (1993: 23, fig. 6P–V), sub *Glandularia macrosperma*.

Distribución geográfica y hábitat. Glandularia macrosperma habita en el centro oeste de la Argentina, desde San Juan, en el norte hasta Chubut al sur. Crece entre los 600 y los 3500 m.

Observaciones. En la descripción original de *Verbena macrosperma* el autor escribe "...estambres absolutamente sin apéndices glandulares...". En el ejemplar tipo se observan estambres con apéndices glandulares muy reducidos; así mismo, todo el material estudiado también presenta esos mismos apéndices. Navas (1979) realiza la combinación de la variedad de Kuntze y la cita para Chile. En el presente tratamiento se considera a *Glandularia sulphurea* var. *intermedia* (Kuntze) L. E. Navas como sinónimo de *G. macrosperma* ya que tanto el material tipo como el material adicional examinado no presenta diferencias significativas para considerarlo un taxón diferente; por otra parte, todos los materiales procedentes de Chile identificados equívocamente, como la variedad anteriormente mencionada, corresponden a *G. sulphurea* var. *sulphurea* (D. Don) Schnack & Covas.

Material adicional examinado. ARGENTINA. **Chubut:** Dpto. Cushamen, Ea. Calcatapul, *Vallerini 1488* (SI); Dpto. Futaleufú, Corcovado-Tecka, *Vallerini 3630* (SI); Dpto. Gastre, entre Gan Gan y Talapaga, *Ruíz Leal 25758* (SI); Dpto. Languiñeo, Quichaura, *Soriano 2270* (SI); Dpto. Río Senguerr, Gdor. Costa-Apeleg, *Vallerini 3806* (SI); Dpto. Tehuelches, 103 km S de Gdor. Costa, *Correa 10382* (SI); Dpto. Telsen, a la salida de Gan-Gan hacia Telsen, *Vallerini 1530* (SI). **Mendoza:** Dpto. Las Heras, Valle Horcones, *Ruíz Leal 157* (SI); Dpto. Malargüe, s. loc., *Burkart 14269* (SI). **Neuquén:** Dpto. Catán Lil, 10 km de La Negra, *Pérez Moreau 3278* (CONC, SI); Dpto. Collón Curá, Sañico, ruta prov. 110, *Schajovskoy s.n. SI 26740* (SI); Dpto. Zapala, Laguna Blanca, *Schajovskoy 89/III SI 25678* (SI). **Río Negro:** Dpto. 25 de Mayo, 11 km de Jacobacci a Maquinchao, *Correa 3693* (SI); Dpto. 9 de Julio, Meseta de Somuncurá, Laguna Raimunda, *Ruíz Leal 25582* (SI); Dpto. Ñorquinco, Ea. Fitalancao, *Vallerini 6339* (SI); Dpto. Pilcaniyeu, a 20 km al S de Paso Flores, *Cabrera 33015* (SI); Dpto. Valcheta, Meseta de Somuncurá, *Troiani 15052* (CTES). **San Juan:** Dpto. Calingasta, del Observatorio El Leoncito al Portezuelo del Tontal, *Kiesling 4655* (SI); Dpto. Iglesia, Reserva de San Guillermo, Cordón del Infiernillo, *Nicora 8569* (SI).

14. Glandularia megapotamica (Spreng.) Cabrera & G. Dawson, Revista. Mus. La Plata, Secc. Bot. 5: 357. 1944. Basiónimo: *Verbena megapotamica* Spreng., Syst. Veg. (ed. 16) [Sprengel] 4(2): 230–231. 1827. TIPO: Brasil. Rio Grande do Sul: s.d., *F. Sellow 13* (lectotipo, aquí designado, K!, K foto SI!).

Verbena phlogiflora Cham. var. *mucilenta* Schauer, Prodr. [DC.] 11: 538. 1847. TIPO: [Brazil.] "Brasilia", s.d., *F. Sellow s.n.* (lectotipo, aquí designado, K 047724!, K foto SI!; isotipos, E 00373264!, F 74529 no visto, F foto SI!).

Sufrútice de 1 m o más de alt., decumbente, ramoso, subglabra, de tallos subcilíndricos o tetrágonos, fistulosos, con pubescencia estrigosa, rala y tenue retrorsa en los tallos, ramas y pedúnculos; entrenudos de 4–10 cm. Hojas con pecíolo de 10–15 mm, lámina de 2.5–7 × 0.8–1.2 cm, enteras, elípticas a angostamente ovadas, submembranáceas, ápice agudo a obtuso, base aguda a cuneada, margen desigualmente serrado, estrigosas a subglabras en ambas superficies. Inflorescencia en pleiobotrios paniculiformes con 1 ó 2 pares de paracladios frondosos, que sobrepasan la florescencia principal, los más distales pueden ramificarse. Florescencias en espigas densas, multifloras, raquis no alargado en la fructificación; entrenudo basal de 8–10 cm; brácteas de 3–5 mm, ovadas a angostamente ovadas, escasamente estrigosas, con glándulas pateliformes, margen ciliado. Flores con cáliz de 10–12 mm, estrigoso y ocasionalmente con glándulas subsésiles pateliformes sobre las costillas, dientes breves, agudos; corola de 13–16 mm, con brevísimos e inconspicuos tricomas glandulares hacia el ápice y en la base de los lóbulos, violácea, fauce pubescente; par superior de estambres con apéndice conectival sin desarrollo de pie; estilo de 13–15 mm. Clusas de 3.8–4.5 mm, ápice cortamente rostrado, base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa reticulosa-venosa, pardo-negruzca, superficie interna blanco-verrucosa.

Iconografía. Troncoso (1971: 615, fig. 1), sub *Glandularia megapotamica*.

Distribución geográfica y hábitat. Glandularia megapotamica habita en el este de Argentina, sur de Brasil, Paraguay y Uruguay. Crece sobre suelos húmedos, pajonales y selvas en galería, a nivel del mar.

Observaciones. Chamisso (1832) describe *Verbena phlogiflora* Cham., basándose en ejemplares de Sellow, de Brasil meridional. En dicha descripción reconoce dos entidades a las que denomina α y β, respectivamente. Posteriormente Schauer (1847: 537) le asigna un nombre a cada una de estas

entidades: α como *V. phlogiflora* var. *mucilenta*, citando como posible sinónimo *V. megapotamica* Spreng.; y β como *V. phlogiflora* var. *vulgaris* Schauer, de esta manera se reconocen válidamente las entidades de Chamisso. Covas y Schnack (1944) realizan la combinación *Glandularia phlogiflora*, sin considerar las variedades de Schauer, sólo tienen en cuenta el nombre propuesto por Chamisso. En el mismo año, pero con posterioridad al trabajo de Schnack y Covas (1944), Cabrera y Dawson (1944: 357), aceptan también el género *Glandularia*, y consideran que tanto *V. megapotamica* Spreng. y *V. phlogiflora*, son iguales. Por tal motivo Cabrera y Dawson (1944), realizan la combinación *G. megapotamica* (Spreng.) Cabrera & G. Dawson, sin reconocer las variedades de Schauer. Moldenke (1964a, 1964b, 1964c, 1964d, 1964e) no reconoce al género *Glandularia* y considera dos especies: *V. megapotamica* (= *V. phlogiflora* var. *mucilenta*, *G. megapotamica*) y *V. phlogiflora* (= *V. phlogiflora* var. *vulgaris*, *G. phlogiflora*), además agrega como sinónimo las dos entidades de Chamisso, las cuales no son válidas. Troncoso (1971), realiza una aclaración sobre este complejo de especies, reconoce a *G. megapotamica* y a *G. phlogiflora* y vuelve a citar en la sinónimia las entidades α y β de Chamisso y las variedades válidas de Schauer. En el presente trabajo se considera que efectivamente *G. megapotamica* es una especie valida y tiene como sinónimo a *V. phlogiflora* var. *mucilenta*, la cual se lectotipifica con el ejemplar de Sellow, de Brasilia porque Schauer al crear la variedad se basa en el material de Sellow visto por Chamisso. Aquí se elige el ejemplar depositado en K, por coincidir exactamente con el protólogo de la especie, además puede leerse en la etiqueta una η, símbolo que Chamisso agregaba cuando se trataba de una nueva especie. El holotipo de *V. megapotamica*, depositado en B, está destruido, razón por la cual se elige como lectotipo el ejemplar depositado en K, por corresponder con el protólogo de la especie.

Glandularia megapotamica es una especie similar a *G. guaranitica*, ver observaciones bajo dicha especie. También es afín a *G. phlogiflora*, de la que se diferencia porque esta última posee el tallo hirsuto-escabroso (vs. subglabra en *G. megapotamica*) y el mayor tamaño de las brácteas (5–6 mm vs. 3–5 mm) y clusas (5–5.5 mm vs. 3.8–4.5 mm).

Material adicional examinado. ARGENTINA. **Buenos Aires:** Pdo. Berisso, Berisso, Los Talas, *Boffa 148* (SI); Distrito Federal, Facultad de Agronomía, *Troncoso 179* (SI); Pdo. Ensenada, Punta Lara, *Cabrera 3401* (LP); Pdo. La Plata, en los pajonales de Los Talas, *Merck s.n.* (SI 3576); Pdo. San Nicolás, Delta del Paraná, Carabelas, *Burkart 4331* (SI); Pdo. Tigre, Delta, *Cabrera 4891* (LP); Pdo. Vicente López, Olivos, *Pastore s.n.* (SI 3572); Pdo. Zárate, Delta del Paraná, Canal Arias y Paraná de las Palmas, *Cabrera 1618* (LP). **Entre Ríos:** Dpto. Paraná, *Boelcke 915* (CTES); Dpto. Gualeguaychú, atacadero Brazo Largo a Puerto Constanza, *Burkart 30103* (SI). **Misiones:** Dpto. Apóstoles, a 10 km de Apóstoles, *Fabris 7356* (LP); Dpto. Capital, s. loc., *Vattuone 60* (BAF); Dpto. Candelaria, Santa Ana, *Llamas 142* (BAF). BRASIL. **Minas Gerais:** Carandí, *Duarte 6309* (SI). PARAGUAY. **Canindeyú:** Aguara Ñu, *Jiménez 1362* (CTES). URUGUAY. **Río Negro:** Ea. Nueva Melhem, *Del Puerto 5746* (SI).

15. Glandularia mendocina (Phil.) Covas & Schnack, Revista Argen. Agron. 11: 96. 1944. Basiónimo: *Verbena mendocina* Phil., Anales Univ. Chile 36: 191. 1870. TIPO: [Argentina.] "Inter mendocina", 1868/69, *R. A. Philippi s.n.* (lectotipo, aquí designado, SGO 54797! [código de barras 4296], SGO 54797 foto SI!; isotipos, SGO 42484! [código de barras 4268], SGO 42484 foto SI!, SI 3939!, US no visto). Figura 5.

Hemicriptófito erecto de 30 cm alt., perenne, erguido, ramificado o no; ramas estrigosas; entrenudos de 2.5–8 cm. Hojas con pecíolo de 5–8 mm, lámina de 3.5–4 × 2–3 cm, contorno ovado-triangular, 3-sectas, bipinnatipartidas, lóbulos lineares, ápice obtuso, superficie adaxial estrigosa, superficie abaxial con mayor concentración de tricomas adpresos sobre las venas, margen revoluto. Inflorescencia en pleiobotrio con 1 ó 2 pares de paracladios generalmente frondosos, que sobrepasan a la florescencia principal. Florescencias en espigas densas, umbeliformes, multifloras, raquis alargado en la fructificación; entrenudo basal de 10–30 mm; brácteas de 4.5–5 mm, estrigosas a híspidas, angostamente ovadas, ápice aristado, margen ciliado. Flores con cáliz de 6–7.5 mm, estrigoso a híspido, principalmente sobre las costillas, pudiendo presentar, al igual que las brácteas glándulas pateliformes, dientes aristados, ca. 1.3 mm; corola de 10–20 mm, lila, rosada, glabra exteriormente, fauce pubescente; par superior de estambres con apéndices conectivales claviformes, inclusos, superando las tecas; estilo de 6–6.5 mm. Cáliz fructífero plegado y retorcido en el ápice; clusas de 3–3.5 mm, ápice redondeado, base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa reticulada, superficie interna papilosa.

Distribución geográfica y hábitat. *Glandularia mendocina* crece en el centro y oeste de Argentina, desde los 600 a los 950 m.

Observaciones. En SGO se encuentran dos ejemplares de este taxón con diferente número de herbario: SGO 54797 y SGO 42484. Pueden considerarse como sintipos, dado que en la etiqueta

de ambos ejemplares puede leerse: "Inter mendocina", tal como se hace referencia en la descripción original (Philippi, 1870: 191). Se elige el ejemplar SGO 54797, como lectotipo porque además de corresponderse con el protólogo, es el más completo. En la descripción original Philippi (1870), aclara que los estambres no tienen apéndices conectivales, lo cual es incorrecto; dado que éstos se observan en el material tipo y el resto del material examinado.

Glandularia mendocina es afín a *G. tenera* y *G. aristigera* principalmente por el contorno, pubescencia y la división de la lámina foliar (ovado-triangular; estrigosa; 3-sectas, bipinnatipartidas), la presencia de glándulas pateliformes en el cáliz y brácteas y la forma angostamente ovada de la bráctea; se diferencian por el hábito (erecto en *G. mendocina*; rastrero en *G. aristigera* y *G. tenera*), por el tamaño de la bráctea y el cáliz (bráctea de 4.5–5 mm, cáliz de 6–7.5 mm en *G. mendocina*; 3–3.5 mm y 9–10 mm en *G. aristigera*; 3.5–4.5 mm y 8–9 mm en *G. tenera*), los apéndices conectivales de los estambres (claviformes y superando las tecas en *G. mendocina*; pequeños y no superando las tecas en *G. aristigera*; cilíndricos y delegados superando la longitud de las tecas en *G. tenera*) y el ápice de la clusa (redondeado; obtuso; apiculado).

Material adicional examinado. ARGENTINA. **Córdoba:** Dpto. Punilla, Gigantes, *Carette 270* (SI). **La Pampa:** Dpto. Rancul, La Maruja, *Burkart 9884* (SI). **Mendoza:** Dpto. La Paz, entre Villa de La Paz y Rancho de Totora, *Ruíz Leal 8497* (SI); Dpto. Luján de Cuyo, La Puntilla, *Covas s.n.* (SI); Dpto. San Rafael, Rincón del Atuel, valle frente gruta del Indio, Rincón del Atuel, *Huajardo 1715* (SI); Dpto. Santa Rosa, Reserva Natural de Ñancuñan, *Ruíz Leal 27181* (SI); Dpto. Tupungato, entre Anchoris y Zapata, *s. coll. 1639* (SI). **San Juan:** Dpto. Valle Fértil, s. loc., *Roig 8382* (SI). **San Luis:** Dpto. Belgrano, 3 km antes de San Antonio, *Roig 8151* (SI); Dpto. La Capital, Alto Pencoso, *Carette 35* (SI).

16. Glandularia microphylla (Kunth) Cabrera, Revista Invest. Agric. 11: 398. 1957. Basiónimo: *Verbena microphylla* Kunth, Nov. Gen. Sp. 2: 272, t. 133. 1818. TIPO: Ecuador. "Crescit in frigidis Regni Quitensis juxta urbem Nova Riobamba, alt. 1482 hex.", s.d., *A. Humboldt & A. Bonpland s.n.* (holotipo, P 00650850!; isotipos, F 74524!, P 650851 no visto, P foto SI!).

Verbena nivea Moldenke, Phytologia 1: 459. 1940. TIPO: Argentina. Salta: Rosario de Lerma, camino a San Antonio, 3000 m, dic. 1929, *S. Venturi 10014* (holotipo, NY 138298 no visto, NY foto SI!; isotipos, LIL 01387! SI 3943!, US 118716 no visto, US no visto).

Verbena nivea Moldenke f. *rosea* Moldenke, Phytologia 8: 60. 1961. TIPO: Argentina. Tucumán: Dpto. Tafí, Cumbre del Cajón, 3800 m, 20 abr. 1926, *S. Venturi 10111* (holotipo, US no visto; isotipos, SI 3920!, US 00118719!).

Sufrútice enano, rizomatoso, de 5–7(–10) cm alt., rastrero, muy ramificado, ramas híspidas de base leñosa; entrenudos de 5–8 mm. Hojas con pecíolo de 1–2 mm, lámina de 0.4–1.6 × 0.4–0.8 cm, contorno ovado, 3-partidas, lóbulos enteros o 2 ó 3 lobados, ápice obtuso, base cuneada; con ambas superficies densamente estrigosas. Inflorescencia principalmente en monobotrio. Florescencias en espigas multifloras densas, raquis alargado en la fructificación; entrenudo basal de 4–10 mm; brácteas de 2.5–3 mm, ovadas, estrigosas en la superficie abaxial, margen ciliado, ápice agudo. Flores con cáliz de 5–7 mm, híspido a estrigoso; dientes triangulares breves; corola de 11–16 mm, blanca, lila, escasamente pubescente en la mitad superior del tubo y a veces en la parte externa de los lóbulos, fauce pilosa; par superior de estambres con apéndices conectivales superando generalmente a las tecas, asomados a la garganta corolar; estilo de 8–9 mm. Clusas de 2.5–3 mm, ápice obtuso, base no angostada y con repliegue basal y transversal de la pared comisural, superficie interna con escasas o abundantes papilas.

Iconografía. Troncoso y Botta (1993: 106, fig. 47F–M), sub *Glandularia microphylla*.

Nombre vulgar. Pastito, vaca, en el ejemplar *Arenas n-802* (SI); yerba del incordio, en los ejemplares *Múlgura 158* (SI), *Ulibarri 1479* (SI); escupe, en el ejemplar *Arenas 1878* (SI); toronjil, en el ejemplar *Biurrum 5189* (CTES, LP).

Distribución geográfica y hábitat. Glandularia microphylla habita en el noroeste de Argentina desde Jujuy a Mendoza; además crece en Bolivia, Ecuador y Perú. Crece en suelos pedregosos de campos secos y valles, entre los 2000 y los 4600 m.

Observaciones. Glandularia microphylla es similar a *G. sulphurea* por el hábito (sufrútice de 20–25 cm vs. 5–10 cm de altura), la longitud del pecíolo (3–5 mm vs. 1–2 mm), las brácteas de 3–3.5 mm, angostamente ovadas y con pubescencia híspido-glandular (vs. 2.5–3 mm, ovadas, estrigosa), corola amarilla y glabra exteriormente (vs. blanca o lila con escasa pubescencia en la mitad superior del tubo y a veces en la parte externa de los lóbulos) y clusas de mayor tamaño (ca. 3.5 mm vs. 2.5–3 mm); la última se diferencia por tener mayor porte, corola amarilla y glabra externamente, cáliz y brácteas híspido-glandulares.

Material adicional examinado. ARGENTINA. **Catamarca:** Dpto. Belén, Cuesta de Randolfo, *Cabrera 32452*

(SI). **Jujuy:** Dpto. Cochinoca, Abra Pueblo de Cochinoca, *Deginani 490* (SI); Dpto. Humahuaca, ruta nac. 9, de Tres Cruces a Humahuaca, Esquinas Blancas, *Cialdella 496* (CTES, SI); Dpto. Ledesma, Alto Calilegua, camino al Cerro Hermoso, *Iudica 120* (SI); Dpto. Rinconada, alrededores de la Laguna Vilama, *Schwabe 796* (LP); Dpto. Santa Catalina, Región de la Puna, *Claren 11468* (BAF); Dpto. Susques, ruta prov. 70, cruce con ruta prov. 16, entre Salina de Olaroz y Coranzulí, *Múlgura 1291* (SI); Dpto. Tilcara, Cerro Alto de Mina al W de Huacalera, *Werner 639* (SI); Dpto. Tumbaya, Abra Portillo, ruta nac. 52, *Nicora 8817* (SI); Dpto. Valle Grande, Santa Ana, *Fabris 3601* (LP); Dpto. Yavi, Abra de Lizoite, *Fabris 7771* (LP). **La Rioja:** Dpto. Vinchina, entre Jagué y Paso Pircas Negras, a 61 km del primero, 1 km de El Peñón, ladera expuesta al E, *Biurrum 5189* (CTES, SI). **Mendoza:** Dpto. San Carlos, 29 km W of jct. with Prov. Rt. 101, on rd. to Laguna Diamante at Gendarme post "Cruz de Piedra", *Olmstead 2004-156* (SI). **Salta:** Dpto. Cachi, camino a Cachi, Piedra del Molino, *Cabrera 30726* (SI); Dpto. Los Andes, San Antonio de los Cobres, *Hunziker 3040* (SI); Dpto. Chicoana, ruta 33, de Cachi a Ciudad de Salta, pasando desvío a ruta 42, *Cialdella 293* (SI); Dpto. La Poma, La Banda, *Cabrera 8866* (LP); Dpto. Rosario de Lerma, Quebrada de Escoipe, Valle Encantado, *Kiesling 1295* (SI). **San Juan:** Dpto. Calingasta, Sierra del Tontal, Cerro Casa de Piedra, *Kiesling 4536* (SI); Dpto. Iglesia, Reserva San Guillermo, al W del Refugio de Agua del Godo, *Kiesling 4577* (SI); Dpto. Ullún, cerros detrás del refugio de la Ea. Don Carmelo, *Kiesling 9082* (SI). **Tucumán:** Dpto. Tafí del Valle, Sierras Calchaquíes, La Puerta, *Burkart 5377* (SI). BOLIVIA. **La Paz:** Inquiasivi, Cordillera Tres Cruces, bajando por Quimo, *Beck 191* (SI). ECUADOR. **Cotopaxi:** Quevedo–Latacunga rd., 26 km E of Pilaló & 71 km W of Latacunga, *Luteyn 6515* (SI). PERÚ. El Belén, *Rea Clavijo 46* (SI).

17. Glandularia nana (Moldenke) Tronc., Darwiniana 19: 738. 1975. Basiónimo: *Verbena nana* Moldenke, Phytologia 3: 119. 1949. TIPO: Argentina. Formosa: Dpto. Pirané, Pirané, 23 Oct. 1945, *I. Morel 117* (holotipo, NY 00138297 no visto, NY foto SI!; isotipos, LIL 001386!, LIL 001385! SI 003097!, US no visto). Figura 6.

Hemicriptófita rastrera de 20–60 cm de alt., erecta, hirsuta-glandulosa; entrenudos de 3.5–6 cm. Hojas con pecíolo de 0.5–1.2 cm, lámina de 2–4 × 1.5–2 mm, ovada a subtriangular, entera, el margen serrado, ápice agudo, base cuneada, ambas superficies estrigosas. Inflorescencia en pleiobotrio heterotéticos con 1 par de paracladios frondosos que sobrepasan o no la florescencia principal, o en monobotrio. Florescencia en espiga multiflora densa, algo alargada a la madurez de los frutos; entrenudo basal de 7–25 mm; brácteas de 3.5–4 mm, angostamente ovadas, híspido-glandulosas sobre la superficie abaxial. Flores con cáliz 9.5–10 mm, híspido glanduloso, dientes ca. 1.5 mm; corola ca. 12 mm, rojiza, rosada, lila, externamente glabra o pubescente, fauce pubescente; par superior de estambres sin apéndice conectival; estilo de 10–10.5 mm. Clusas de mayores de 5.5 mm,, ápice apiculado, base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa reticulada hacia el ápice (1/3) el resto acanaladas.

Nombre vulgar. Tiburcia roja en el ejemplar *Gilbert s.n.* (CTES 408677); verbena de los palmares, en el ejemplar *Meyer 680* (SI).

Distribución geográfica y hábitat. Glandularia nana habita en el norte y este de Argentina y sur de Brasil y Paraguay. Crece en suelos salino-arcillosos, terrenos húmedos, pastizales y campos ribereños.

Observaciones. Glandularia nana es una especie similar a *G. peruviana* y *G. tweedieana*, por el hábito rastrero, las hojas enteras y los estambres sin apéndices conectivales; estas dos especies se diferencian de *G. nana*, por las clusas de menor tamaño (ca. 6 mm en *G. nana*; 4–4.5 mm y 4.5–5 mm en *G. peruviana* y *G. tweedieana*, respectivamente), la pubescencia de la cara abaxial de la hoja es estrigosa (vs. híspida en *G. peruviana* y cano-hispídula en *G. tweedieana*). También suele confundirse con *G. hassleriana*, ver observaciones bajo dicha especie.

Material adicional examinado. ARGENTINA. **Chaco:** Dpto. 1° de Mayo, Margarita Belén, *Schulz 11309* (CTES), *Martínez 9693* (SI); Dpto. Cmte. Fernández, EEA Sáenz Peña, *Gilbert s.n. CTES 408677* (CTES); Dpto. Gral. Güemes, 1 km de Castelli en dirección E, por ruta que une Castelli–El Asustado, *Fortunato 1272* (SI); Dpto. Independencia, Avia Teray, *Castellanos s.n. BA 30/1753* (SI); Dpto. Mayor Fontana, *Meyer 680* (SI); Dpto. O'Higgins, 1 km N La Tigra, ruta vieja, *Bordón s.n. CTES 408675* (CTES). **Corrientes:** Dpto. Mburucuyá, Estancia Santa Teresa, *Burkart 31065* (SI); Dpto. Santo Tomé, Arroyo Chimiray, *Krapovickas 26138* (SI). **Formosa:** Dpto. Formosa, ruta nac. 11 vieja, al N de Ayo. Francesa Cué, *Guaglianone 286* (SI); Dpto. Patiño, Bartolomé de las Casas, área Experimental Vinal, *Schulz 17618* (CTES); Dpto. Pilcomayo, riacho Eh Eh, ruta nac. 11, *Krapovickas 13087* (SI). **Misiones:** Dpto. Apóstoles, San José, Escuela Agrotécnica Pascual Gentilini, *Cabrera 29258* (SI); Dpto. Leandro N. Alem, ruta nac. 14, Gral. Güemes, *Cabrera 29333* (SI); Dpto. San Ignacio, San Ignacio, *Martínez Crovetto 11392* (CTES); Dpto. San Pedro, s. loc., *Montes 15434* (SI). BRASIL. **Mato Grosso do Sul:** Corumbá, Fazenda Acurizal, Nabileque, Pantanal, *Pott 3866* (SI). **Rio Grande do Sul:** Quaraí, Serra Javaó, *Pedersen 12556* (SI). **Santa Catarina:** Araranguá, Curralinhas, *Reitz C. 882* (SI). PARAGUAY. **Alto Paraguay:** Puerto Fonciere, *Rojas 14061* (SI). **Boquerón:** Puerto Casado & vic., near Estancia "Guajhó", *Pedersen 4069* (SI). **Guairá:** Iturbe, *Montes 12429* (SI). **Misiones:** 12 km W de San Ignacio, camino a Pilar, *Arbo 1903* (SI). **Presidente Hayes:** Misión San Leonardo de Escalante, *Sturzenegger s.n.* (BACP 2433, SI).

18. Glandularia parodii Covas & Schnack, Revista. Argent. Agron. 11: 96, fig. 3. 1944. *Verbena parodii* (Covas & Schnack) Moldenke, Phytologia 2: 149. 1946. TIPO: Argentina. Mendoza:

Dpto. Tupungato, entre Achoris y Zapata, 5 mar. 1944, *G. Covas & B. J. C. Schnack 2112* (holotipo, SI 3806!; isotipos, SI 3805!, SI 3007!).

Hemicriptófito rastrero, con ramas floríferas erectas, de 20–30 cm alt. Ramas híspidas con algunos tricomas glandulares; entrenudos de 2–3.5 cm. Hojas con pecíolo de 0.9–1.2 cm, lámina de 1–3.5 × 0.7–2.5 cm, contorno triangular, 3- ó 5-secta, bipinnatisectas, segmentos ca. 1 mm lat., filiformes, margen apenas revoluto; superficies híspidas a adpresas, con tricomas largos blanquecinos. Inflorescencia principalmente en monobotrio, cuando pleiobotrios el par de paracladios es débil y generalmente no sobrepasa la florescencia principal. Florescencias en espigas densas, multifloras, raquis alargado en la fructificación; entrenudo basal de 20–40 mm; brácteas de 4–6 mm, ovado angostas, híspidas, de ápice agudo, el margen ciliado. Flores con cáliz de 5–8 mm, híspido sobre las costillas, tricomas largos, dientes abaxiales de 1 mm; corola de 10–16 mm, blanca-lilácea, violeta claro, con pubescencia variable externa, fauce pubescente; par superior de estambres con apéndices conectivales mayores a las tecas, asomando en la corola; estilo de 8–9 mm. Cáliz fructífero contorto en la zona apical; clusas de 3–5 mm, cilíndricas, con apículo desarrollado o no, base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa reticulada, superficie interna papilosa.

Iconografía. Botta (1993: 23, fig. 6A–N), sub *Glandularia parodii*.

Nombre vulgar. Calvagloria, en el ejemplar *s. coll. s.n.* (SI); margarita dulce en Covas (1966: 91) y en ejemplar *Burkart 19221* (SI); margarita morada en el ejemplar *Osten 2748* (SI).

Distribución geográfica y hábitat. Glandularia parodii habita en el centro y sur de la Argentina. Crece en los bordes de camino, ecotono espinal-bosque, pastizales, entre los 200 y los 3700 m.

Observaciones. Glandularia parodii es una especie similar en hábito, división foliar y ápice de las clusas a *G. tenera*; esta última puede diferenciarse por las brácteas con el nervio central evidente y de menor tamaño (3.5–4.5 mm vs. 4–6 mm en *G. parodii*), por la pubescencia estrigosa del cáliz, bráctea y lámina foliar (vs. híspido en *G. parodii*), además en *G. tenera* es muy frecuente la presencia de glándulas pateliformes distribuidas en las brácteas y el cáliz.

Material adicional examinado. ARGENTINA. **Buenos Aires:** Pdo. Azul, entre Azul y Olavarría, puente sobre río Azul, *Fabris 2686* (SI); Pdo. Olavarría, Campo Saraillet, *Osten 2748* (SI); Pdo. Patagones, 20 km al N de Patagones, *Cabrera 19583* (SI); Pdo. Villarino, Pedro Luro, a orillas del canal de riego, *Hunziker 4584* (SI). **Chubut:** Dpto. Biedma, península Valdés, Punta Hércules, *Nicora 8414* (SI). **Córdoba:** Dpto. Ascochinga, San Marcos, *Nicora 2358* (SI); Dpto. Punilla, San Esteban: *Nicora 1526* (SI); Dpto. San Esteban, San Esteban a La Cumbre, *Nicora 19553* (SI). **La Pampa:** Dpto. Caleu-Caleu, 80 km al N del empalme con ruta nac. 22 (Anzoátegui) a Río Colorado, *Ruíz Leal 25496* (SI); Dpto. Loventue, Loventue, Carro Quemado, *Cano 2686* (SI); Dpto. Lihuel *Calel*, frente a Sierra de Lihuel Calel, en camino a Gral. Acha, *Ruíz Leal 26042* (SI); Dpto. Rancul, entre Chamaico y Casimiro Gómez, *Cabrera 19390* (SI); Dpto. Toay, en camino que une ruta 14 con ruta 5, *Cano 3394* (SI); Dpto. Utracán, 39 km E de la Reforma, *Rossow 1518* (SI). **Mendoza:** Dpto. Las Heras, entre El Peral y Chacras de Coria, *Covas 296* (SI); Dpto. Luján de Cuyo, Anchoris, *Covas s.n.* (SI); Dpto. San Carlos, Cruz de Piedra, *H. A. L. 7255* (SI); Dpto. San Rafael, ruta prov. 190, 20 km E de Punta de Agua, *Prina 2700* (CTES, SI); Dpto. Tupungato, s. loc., *Ruíz Leal 1167* (SI). **Río Negro:** Dpto. Adolfo Alsina, ruta nac. 3, Km 1107, entre Viedma y San Antonio Oeste, *Correa 2456* (SI); Dpto. Avellaneda, Isla Choele Choel, al W de Luis Beltrán, *Correa 9726* (SI); Dpto. Conesa, a 55 km de Conesa, desde Río Colorado, *Ruíz Leal 25911* (SI); Dpto. Gral. Roca, Altiplano de Chelforó a Chichinales, *Rasp 193* (SI); Dpto. Pichi-Mahuida, afueras de Río Colorado, *Correa 9738* (SI); Dpto. San Antonio, 42 km E de San Antonio Oeste, *Correa 10131* (CTES). **San Juan:** Dpto. Calingasta, El Pachón, *Kiesling 8108* (SI); Dpto. Valle Fértil, de las Tumanas a Balde del Rosario, *Ahun 29* (SI). **San Luis:** Dpto. Chacabuco, Estanzuela, *Múlgura 1135* (SI); Dpto. Gral. Pedernera, Villa Mercedes, 2 km al E en banquina de ruta 8, *Anderson 1810* (SI); Dpto. Gdor. Dupuy, R 148, entre Nueva Galia y Arizona, *Cano 2590* (SI); Dpto. La Capital, ruta nac. 7 Alto Pencoso, *Cano 2715* (SI); Dpto. Pringles, ruta 7, Km 673, *Cabrera 29513* (SI).

19. Glandularia peruviana (L.) Small, Manual S. E. Fl., 1139. 1933. Basiónimo: *Erinus peruvianus* L., Sp. Pl. 2: 630. 1753. *Verbena peruviana* (L.) Britton, Ann. New York Acad. Sci. 7: 197. 1893. TIPO: [Paraguay.] Tab. XXV, fig. 3 en L. Feuillée, J. Obs. Phys. Math. Bot. [3]: 36. 1725 (lectotipo, designado por Moldenke [1964d: 319]).

Verbena melindres Gillies, Bot. Reg. 14: 1184. 1828. *Verbena chamaedryfolia* Juss. var. *melindres* (Gillies) Schauer, Prodr. (DC.) 11: 537. 1847. TIPO: [Argentina.] "Pampas of Buenos Ayres", tab. 1184 en Bot. Reg. 14. 1828 (lectotipo, aquí designado, tab. 1184 en Edwards, 1828).

Verbena melindroides Cham., Linnaea 7: 270. 1832. *Verbena chamaedryfolia* Juss. var. *melindroides* (Cham.) Schauer, Prodr. (DC.) 11: 537. 1847. TIPO: Brazil. Santa Catarina, s.d., *F. Sellow s.n.* (lectotipo, aquí designado, K 470559!, K foto SI!).

Verbena sanguinea Larrañaga, Escritos Damaso Antonio Larranaga 2: 9. 1923. TIPO: Lámina XLII en Escritos Damaso Antonio Larranaga 2: 9. 1923 (lectotipo, aquí designado, pl. XLII en Larrañaga [1923: 9]).

Hemicriptófita rastrera, con tallos a veces radicantes en los nudos basales, hirsutos y con tricomas glandulares más cortos; entrenudos de 1.5–4 cm. Hojas subsésiles a pecioladas, con pecíolo de 3–13 mm, lámina de 0.5–3(–3.5) × 0.4–1.5 cm, enteras, ovada a elíptica, ápice y base cuneada, margen regular o irregularmente crenado o serrado; cara adaxial estrigosa, cara abaxial híspida, más densamente sobre los nervios. Inflorescencias principalmente en monobotrios. Florescencias en espigas, densas multifloras, raquis alargado en la fructificación; entrenudo basal de 4–7 cm, densamente hirsuto-glanduloso; brácteas de 3.5–4.5 mm, ovadas a angostamente ovadas, de ápice agudo, pubescente-glandulosa en la cara externa y con tricomas más largos en el margen. Flores con cáliz de 9–11 mm, hispídulo-glanduloso, más densamente sobre las costillas, dientes ca. 0.5 mm, triangulares, muy breves; corola de 13–15 mm; rojo carmín, en general glabra exteriormente, fauce pilosa, lóbulos de ápice obtuso, emarginado; par superior de estambres sin apéndices conectivales; estilo de 9–11 mm. Clusas de 4–4.5 mm, rectas, ápice obtuso, base no angostada y con repliegue basal y transversal de la pared comisural.

Nombre vulgar. Margarita punzó, camaradinha, margarita colorada, margarita del campo, melindre, verbena roja (Moldenke & Moldenke, 1949).

Usos y parte usada. La hoja es usada como antiespasmódico, estomacal, oftalmológico y detersorio (Toursarkissian, 1980; Novara, 1984; Orfila & D'Alfonso, 1999; Nuñez & Cantero, 2000; Barboza et al., 2006).

Distribución geográfica y hábitat. *Glandularia peruviana* está ampliamente distribuida en el centro y norte de Argentina, también en Bolivia, Brasil, Paraguay y Uruguay. Crece en suelos con afloramientos rocosos, pedregosos o suelos arenosos, de bordes de caminos, campos abiertos pastizales de altura, también sobre terrenos húmedos, entre el nivel del mar y los 3000 m.

Observaciones. De acuerdo con Briquet (1904a), Linnaeus (1753: 630) basó su especie *Erinus peruvianus* en "...Lychnidaea veronicae folio, flore coccíneo...", de Feuillée, quien colectó el ejemplar tipo en Paraguay, no en Perú como lo cita Linnaeus. *Verbena peruviana* (L.) Druce (Druce, 1914: 425) es un nombre superfluo dado que la combinación ya había sido efectuada por Britton (1893). El holotipo de *V. melindroides*, depositado en B se encuentra destruido, por tal motivo se elige como lectotipo el ejemplar de K 470559, por corresponderse con el protólogo de la especie. *Verbena chamaedryfolia* Juss. (Jussieu, 1806: 73) es un nombre ilegítimo por que entre sus sinónimos se encuentra *Erinus peruvianus* L. En esta obra Jussieu intentó establecer un nuevo nombre para *E. peruvianus* por considerar que el epíteto específico no concuerda con la descripción geográfica. *Verbena chamaedryfolia* L. ex Lorentz, es un nomen nudum, ya que Lorentz (1878) cita de forma errónea el autor de la especie. *Verbena coccinea* Reider (Reider, 1831: 288) es otro nomen nudum, como también lo es *V. veronicaefolia* Sm. (apud Steudel, 1841: 750) [non *V. veronicaefolia* Humb., 1825], nom. nud. de acuerdo a información brindada por el Dr. Eduardo Alonso Paz (MVM), todo el material tipo de Larrañaga se ha destruido en Montevideo, Uruguay, por lo tanto se elige como lectotipo de *V. sanguinea* Larrañaga la iconografía de la descripción original (Larrañaga, 1923). En el caso de *V. melindres* Gillies es necesario lectotipificar, dado que el autor no cita material de herbario, pero ilustra la especie.

Glandularia peruviana es una especie muy similar a *G. tweedieana*, por el hábito, color de la corola, forma y tamaño de las clusas, estambres sin apéndices, ambas especies se diferencian por tener las hojas dimorfas y pubescencia cano-hirsuta.

Material adicional examinado. ARGENTINA. **Buenos Aires:** Pdo. Ante. Brown, Claypole, F.C.S., *Vattuone s.n.* (BAF); Pdo. Balcarce, entre San Agustín y las Nutrias, *Grondona 7057* (CTES); Pdo. Campana, Campana, *Valencia 14925* (SI); Pdo. Carlos Casares, C. Casares, ruta nac. 5, *Krapovickas 22288* (CTES, SI); Pdo. Cnel. Suárez, s. loc., *Burkart 28194* (SI); Pdo. Gral. J. Madariaga, Juancho, *Cabrera 3388* (LP); Pdo. Gral. Pinto, s. loc., *Hicken s.n.* (SI 3346); Pdo. Gral. Pueyrredón, Mar del Plata, *Carette 504* (SI); Pdo. Juárez, Sierra de la Tinta, Cerro El Sombrerito, *Abbiatti 4462* (LP); Pdo. La Plata, Gorina, *Zardini 524* (LP); Pdo. Lincoln, s. loc., *s. coll. s.n.* (LP); Pdo. Magdalena, Punta de Indio, mitad camino a Magdalena, *Fabris 2506* (LP); Pdo. Morón, Ituzaingó, *Holmberg s.n.* (SI 10449); Pdo. Olavarría, Olavarría, *Villamil 3131* (CTES); Pdo. Pehuajó, Magdala, *Cabrera 10250* (SI); Pdo. Pellegrini, entre Mari-Lauquén y Bocayuna, *Cabrera 7968* (SI); Pdo. Saavedra, Cerro Curamalal Grande, *Villamil 2573* (SI); Pdo. Saladillo, hacia Sojo, *Múlgura 3490* (SI); Pdo. San Vicente, San Vicente, *Burkart 13462* (SI); Pdo. Tandil, Los Leones, *Pastore 1199* (SI); Pdo. Tornquist, Sierra de la Ventana, *Kiesling 1925* (SI); Pdo. Tres Arroyos, Ea. Santa Felisa, *Villamil 4382* (CTES); Pdo. Tres de Febrero, Martín Coronado, *Nicora 2007* (SI). **Catamarca:** Dpto. Ambato, ruta nac. 62, Km 1460, *Burkart 26566* (SI); Dpto. Andalgalá, Valle de Las Estancias, *Slanis 167* (SI); Dpto. del Alto, Balcuzna, *Venturi 7164* (SI). **Chaco:** Dpto. 1° de Mayo, Colonia Benítez, *Schulz 1476* (CTES); Dpto. Cnte. Fernández, Roque Saens Peña, *Schulz s.n.* (CTES); Dpto. Gral. Güemes, Nueva Pompeya, en la rivera N del brazo del río Teuco, *Fortunato 6430* (CTES). **Córdoba:** Dpto. Calamuchita, Río Tercero, *Krapovickas 6408* (SI); Dpto. Colón, frte. planta de agua mineral, *Galetto 64* (SI); Dpto. Cruz del Eje, Cruz del Eje, *Boffa 1093* (LP); Dpto. Ischilín,

Dean Funes, *Nicora 17724* (SI); Dpto. Pocho, subida W de la Sierra de Pocho, *Cabrera 29634* (SI); Dpto. Pte. Roque Saenz Peña, camino de Rufino a Lag. Del Monte, *Sayago 2370* (SI); Dpto. Punilla, San Esteban, *Nicora 1558* (SI); Dpto. Río Cuarto, Río Cuarto, Achiras, *Trelles 3352* (SI); Dpto. San Javier, La Paz, "Loma Bola", camino a lo largo del arroyo "El Parral", *Lichtenstein s.n.* (SI 18104); Dpto. Santa María, Carlos Paz, *Galetto 75* (SI); Dpto. Río Seco, La Pintada, Cerro de San Miguel, a 12 km de Villa María, *Cano 1917* (BAF). **Corrientes:** Dpto. Bella Vista, R 27, 10 km S de Bella Vista, Toropí, *Schinini 9866* (CTES, SI); Dpto. Capital, Puente Pesoa, ayo. Riachuelo, *Schinini 6824* (CTES); Dpto. Concepción, 6 km E de Santa Rosa, Estancia Millán, *Arbo 909* (SI); Dpto. Empedrado, ruta nac. 12, Km 958, Ayo. San Lorenzo, *Morrone 5323* (SI); Dpto. Esquina, Guayquiraró, *Quarín 2124* (CTES); Dpto. Gral. Paz, lomas de Vallejos, *Schinini 7012* (CTES); Dpto. Goya, S de Goya, *Schulz 16593* (CTES); Dpto. Ituzaingó, *Spegazzini 10410* (BAF); Dpto. Mburucuyá, Parque Nac. Mburucuyá, *Cocucci 3093* (CTES); Dpto. Salado, 2 km al S de Rincón de Ambrosio, *Cáceres 113* (CTES); Dpto. San Cosme, camino a Puerto González, ruta prov. 1, *Pérez 145* (CTES); Dpto. San Luis del Palmar, 19.5 km SE de San Luis del Palmar, *Schinini 31285* (CTES); Dpto. San Miguel, 12 km NE de San Miguel, Ea. Toro-y, *Vanni 1558* (CTES); Dpto. Santo Tomé, Ayo. Chimiray, *Schinini 6805* (CTES, SI). **Entre Ríos:** Dpto. Colón, Parque Nac. El Palmar, *Botta 272* (SI); Dpto. Concordia, Salto Grande, Casa de Piedra, *Bottino 16* (CTES); Dpto. Diamante, 20 km en ruta a Paraná, *Burkart 22281* (SI); Dpto. Gualeguaychú, pasando Ceibas, *Botta 252* (SI); Dpto. La Paz, Puerto Marquez, *Troncoso 3036* (SI); Dpto. Paraná, Parque Nac. Gral. San Martín, *Correa s.n.* (SI 18071); Dpto. Uruguay, Concepción del Uruguay, *Burkart 17961* (SI); Dpto. Villaguay, camino de Paraná a Villaguay, 5 km desde Arroyo Sauce Grande, *Naranjo 758* (SI). **Formosa:** Dpto. Bermejo, Laguna Yerma. Est. Exp. Laguna Yerma, *Vanni 4292* (CTES); Dpto. Matacos, Ingeniero G. N. Juárez, *Arenas 2378* (CTES); Dpto. Patiño, 17 km al W de Las Lomitas, por ruta nac. 81, *Fortunato 6818* (CTES); Dpto. Pilcomayo, Laguna Blanca, borde sur, *Piccinni 2565* (CTES). **Jujuy:** Dpto. Doctor Manuel Belgrano, camino de San Salvador de Jujuy a La Almona, *Aramayo 14* (SI); Dpto. Ledesma, Sierra de Calilegua, *Venturi 5270* (SI); Dpto. Sta. Bárbara, Sierra El Centinela, 2100 m, *Cabrera 17331* (SI); Dpto. Tilcara, Jardín Botánico de Tilcara, *Burkart 30609* (SI); Dpto. Tumbaya, Volcán al S, *Kiesling 5112* (SI); Dpto. Valle Grande, 2–4 km al S de Valle Grande, *Hunziker 12754* (SI). **La Pampa:** Dpto. Guatraché, entre Perú y Guatraché, *Solbrig 156* (SI); Dpto. Maracó, entre Gral. Pico y Trebolares, ruta nac. 143, *Troiani 3446* (SI); Dpto. Toay, Parque Luro, *Ruíz Leal 26039* (SI); Dpto. Utracán, Gral. Acha, *Orbea s.n.* (SI 18724). **La Rioja:** Dpto. Capital, Sierra de Velazco, cima cerro de la Cruz, *Biurrum 2546* (CTES); sin dpto., quebrada del Portezuelo, camino a la mina, *Hunziker 5107* (SI). **Mendoza:** Sin dpto., Sierra de Los Padres, *Lanfranchi 1717* (SI). **Misiones:** Dpto. Apóstoles, entre San José y Apóstoles, *Zuloaga 968* (SI); Dpto. Cainguás, Puerto Rico, *Montes 3989* (CTES, LP); Dpto. Candelaria, entre Santa Ana y Oberá, a 10 km de ruta 12, *Zuloaga 645* (SI); Dpto. Capital, Posadas, *Gianelli s.n.* (SI 3573); Dpto. Concepción, Ea. de Elsa Prates sobre el río Uruguay, *Biganzoli 1661* (SI); Dpto. Leandro N. Alem, Güemes, entre San José y Cerro Azul, *Cabrera 28627* (SI); Dpto. Ldor. Gral. San Martín, Predio UNLP, valle del Arroyo Cuña Pirú, ruta 7 hacia Aristóbulo del Valle, ca. la entrada al balnerio, *Biganzoli 91* (SI); Dpto. San Ignacio, camino de acceso a finca Osonunú, *Múlgura 2119* (SI); Dpto. San Javier, 30 km de Leandro N. Alem, camino a San Javier, sobre ruta prov. 4, *Krapovickas 15163* (CTES). **Salta:** Dpto. Anta, Parque Nac. El Rey, *Brown 284* (SI); Dpto. Cerrillos, La Pedrera, *Novara 2121* (SI); Dpto. Guachipas, Cuesta del Lajar, ruta nac. 9, 23 km al SE de Guachipas, *Novara 9418* (SI); Dpto. La Capital, Cobos, *Cabrera 12763* (SI); Dpto. La Viña, ruta nac. 68, 6 km al S de La Viña, camino a Cafayate, *Zuloaga 7884* (SI); Dpto. Metán, ruta prov. 34, 78 km N de Metán, *Cordo s.n.* (SI); Dpto. Rivadavia, 3 km de Rivadavia, sobre el antiguo cauce del Bermejo, *Saravia Toledo 1405* (SI). **San Luis:** Dpto. La Capital, Volcán, en cerros saliendo del pueblo hacia Trapiche, *Seijo 1746* (CTES); Dpto. Chacabuco, ruta prov. 1, arroyo La Aguada, *Múlgura 1129* (SI); Dpto. Cnel. Pringles, de La Toma a San Martín, *Kiesling 1065* (SI); Dpto. Gral. Pedernera, Villa Mercedes, *Nicora 4817* (SI). **Santa Fé:** Dpto. 9 de Julio, Tostado, *Ragonese 2397* (SI); Dpto. Castellanos, Rafaela, *Kiesling 5071* (SI); Dpto. Gral. Obligado, Berna, *Ragonese 2606* (SI); Dpto. La Capital, entre Laguna Paiva y Arroyo Aguilar, *Ragonese 2042* (SI); Dpto. San Cristóbal, entre el río Calchaquí y la Ea. "La Alicia", *Ragonese 3007* (SI); Dpto. San Jerónimo, Riacho Coronda, frente a Pto. Gaboto, *Morello 16931* (SI); Dpto. Vera, ruta prov. 38, 10 km antes de La Gallareta, *Deginani 1868* (SI). **Santiago del Estero:** Dpto. Guasayán, de Luján a Santa Catalina, *Rotman 261* (SI); Dpto. Ojo de Agua, Sierra de Sumampa, ruta nac. 9, *Piccinnini 3850* (CTES); Dpto. Moreno, ruta nac. 89 a 70 km al E de Quimilí, *Eskuche 3087-26* (SI). **Tucumán:** Dpto. Burruyacú, Río Nio, *Burkart 26530* (CTES, SI); Dpto. Capital, *Schulz 2887* (CTES); Dpto. Cruz Alta, camino a Alderete, *Correa 188* (SI); Dpto. Leales, Chañar Pozo, *Venturi 378* (SI); Dpto. Tafí, Tafí, *Botta 371* (SI); Dpto. Tafí del Valle, ruta a Tafí del Valle, a la altura de La Angostura, *Galetto 153* (SI). BOLIVIA. **Chuquisaca:** Luis Calvo, Villamontes, 70 km hacia Camiri, *Beck 9773* (SI). **Santa Cruz de la Sierra:** Cordillera, Charagua, 18 km al E, camino a Colonias Menonitas, *Martínez 12490* (CTES). **Tarija:** Cercado, Tarija, 29 km hacia Palos Blancos, *Beck 22163* (SI). BRASIL. **Rio Grande do Sul:** Santa María, Fazenda Santa María, *Moreira Filho 353* (CTES). **Santa Catarina:** Araranguá, Morros dos Conventos, *Hatschbach 1993* (CTES). PARAGUAY. **Caaguazú:** Arroyo Guaranungua, 28 km S of Arroyo Yhú, *Zardini 24654* (SI). **Canindeyú:** Mbaracayú Biosphere Reserve, Aguará Ñu, *Zardini 60286* (SI). **Central:** Asunción, *Arenas 412* (SI). **Cordillera:** Tobatí, Cerro Tobatí, *Degen 343* (SI). **Guairá:** Villarica, *Jörgensen 3772* (SI). **Itapúa:** Cordillera San Rafael, Distr. Alto Vera, *Gonzáles 444* (CTES). **Misiones:** Santiago, Estancia La Soledad, *Pedersen 9585* (SI). **Paraguarí:** Paraguarí, Compañía Costa Segunda, Cerro Palacios, *Zardini 3071* (SI). **Presidente Hayes:** Pozo Colorado, *Zardini 59910* (SI). URUGUAY. **Cerro Largo:** Palleros, *Rosengurtt 1428* (SI). **Colonia:** Riachuelo, *Fabris 9* (LP). **Florida:** Río Jí y A° Mansavillagra, *Rosengurtt b749* (SI). **Montevideo:** La Teja, *Felippone 3271* (SI). **Paysandú:** Esc. de Agron., *Rosengurtt b891* (SI). **Salto:** Picada de Pereyra, *Rosengurtt b1012* (SI).

20. Glandularia phlogiflora (Cham.) Schnack & Covas, Darwiniana 6: 475. 1944. Basiónimo: *Verbena phlogiflora* Cham., Linnaea 7: 266. 1832. *Verbena phlogiflora* var. *vulgaris* Schauer, Prodr. (DC.) 11: 538. 1847, como var. β. *Verbena megapotamica* var. *phlogiflora* (Cham.)

Kuntze, Revist. Gen. Pl. 3(2): 256. 1898. TIPO: Brazil. s. loc., s.d., *F. Sellow s.n.* (lectotipo, aquí designado, G!; isotipos, E 00373265!, K 470726 no visto, K foto SI!, US no visto, SI!).

Verbena phlogiflora Cham. f. *alba* Moldenke, Phytologia 4: 184. 1953. TIPO: Brazil. Santa Catarina: São Joaquim, in a campo Cambajuva, 1200 m, 23–29 ene. 1950, *P. R. Reitz 3443* (holotipo, NY 138310 no visto, NY foto SI!; isotipos, S no visto, S foto SI!, SI 3802!).

Verbena hassleriana Briq. var. *ovatifolia* Moldenke, Phytologia 6: 330. 1958, syn. nov. TIPO: Brazil. Santa Catarina: Rio Negrinho, Ruderal Rio Negrinho, 8 dic. 1956, *L. B. Smith 8478* (holotipo, TEX-LL no visto, TEX-LL foto SI!; isotipos, SI 003790!, US no visto, US foto SI!, US no visto).

Sufrútice suberecto de 40–70 cm alto, o semidecumbente, por lo general extendida o apoyante hirsútulo-escabrosa, muy ramificada; ramas subtetrágonas subfistulosas, débiles, hirsútulas, con pelitos rígidos extendidos o retrorsos y glandulares más breves; entrenudos de 4–8.5 cm. Hojas con pecíolo de hasta 20 mm, lámina de 2–7 × 0.7–2.5 cm, enteras, ovadas, ápice agudo, base cuneada o a truncada, márgenes desigualmente inciso-serrado, excepto en la porción basal, cara adaxial estrigosa, hirsuta sobre los nervios, el resto con pelitos más breves igualmente rígidos, cara abaxial híspida. Inflorescencia en monobotrio o pleiobotrios con 1 ó 2 pares de paracladios, raquis no alargado en la fructificación; brácteas angostamente ovadas, de 5–6 mm, pestañosas y escasamente hirsutas sobre el nervio medio y con pocos pelitos glandulares. Flores con cáliz de 12–16 mm, híspido con pelitos glandulares breves sobre las costillas, dientes desiguales subulados, con largos tricomas extendidos; corola de 18–20 mm, violáceo-purpúreas, con brevísimas glándulas, inconspicuas a simple vista, en la mitad superior del tubo corolar y cara inferior de los lóbulos, fauce pubescente; par superiores de estambres con apéndices conectivales, inclusos, sésiles; estilo de 17–18 mm. Clusas de 5–5.5 mm, cilíndricas, ápice subrostrado, base no ensanchada y con repliegue basal y transversal de la pared comisural.

Iconografía. Troncoso (1971: 617, fig. 2), sub *Glandularia phlogiflora*.

Nombre vulgar. Margarita, Mr. Tweedie's vervain, canaradinha (Moldenke, 1964e: 498).

Distribución geográfica y hábitat. Glandularia phlogiflora crece en el este de Argentina, y sur de Brasil y Paraguay. Habita en suelos húmedos en selva marginal, entre los 200 y los 1200 m.

Observaciones. Chamisso establece la especie *Verbena phlogiflora* sobre la base de varios ejemplares de Sellow y distingue dos entidades α y β. Schauer reconoce *V. phlogiflora* y crea dos variedades que se corresponden a las entidades mencionadas por Chamisso: *V. phlogiflora* var. *vulgaris* Schauer, considerada aquí como la variedad típica, y *V. phlogiflora* var. *mucilenta* Schauer, sinónimo de la actual *Glandularia megapotamica* (Spreng.) Cabrera & G. Dawson (ver observaciones bajo *G. megapotamica*).

De los sintipos de Sellow distribuidos en varios herbarios se designa como lectotipo el ejemplar visto por Chamisso y posteriormente por Schauer (1847: 538) en cuya etiqueta puede leerse: "*V. phlogiflora η var. β, Sellow, Brasilia*", por corresponderse exactamente con el protólogo y considerar que Chamisso agregaba una *η* a continuación del nombre de la nueva especie que describía.

Glandularia phlogiflora es una especie muy afín a *G. guaranitica* y *G. megapotamica*, ver observaciones bajo la primera.

Material adicional examinado. ARGENTINA. **Buenos Aires:** Pdo. Zárate, Delta del Paraná, Arroyo Manzano de Medina, *Bridarolil 2564* (LP). **Corrientes:** Dpto. Ituzaingó, Playadito, 20 km W de Apóstoles, *Schinini 21821* (CTES). **Misiones:** Dpto. Apóstoles, 12 km de Apóstoles, *Fabris 7350* (LP); Dpto. Capital, Nemesio Parma, *Daviña 511* (CTES); Dpto. Gral. M. Belgrano, 15 km al NW de Bernardo de Irigoyen, *Fabris 7435* (LP); Dpto. San Ignacio, s. loc., *Molfino s.n.* (BAF); Dpto. San Pedro, Reserva de Biósfera Yabotí, al N del Parque Prov. Esmeralda, camino a aldea aborigen Yabotí miní, *Keller 2830* (CTES). BRASIL. **Mato Grosso:** Rio Brilhantes, Fda. Bela Vista, *Hatschbach 26081* (SI). **Paraná:** Bituruna, Rio Jangada, *Hatschbach 14967* (SI). **Rio Grande do Sul:** Porto Alegre, Morro da Policia, *Rambo 37693* (SI). **Santa Catarina:** Riqueza, rocky banks & stream bed, Río Iracena, E of Riqueza, *Smith 12592* (LP). PARAGUAY. **Guairá:** Terreno de la Azucarera Paraguaya, *Schinini 1DB* (SI). **Itapúa:** Yacyreta dam island reserve, *Zardini 59148* (SI).

21. Glandularia platensis (Spreng.) Schnack & Covas, Darwiniana 6: 475. 1944. Basiónimo: *Verbena platensis* Spreng., Syst. Veg. (ed. 16) [Sprengel] 2: 748. 1825. TIPO: Brazil. s.d., *F. Sellow s.n.* (neotipo, aquí designado, P!; isotipo, SI!).

Verbena teucrioides Gillies & Hook. ex Hook., Bot. Misc. 1: 167. 1829. TIPO: Argentina. "Mountains Mensoza", *C. B. Gillies s.n.* (lectotipo, aquí designado, E 00259074 no visto [imagen digital!]).

Verbena scordioides Cham., Linnaea 7: 269. 1832. TIPO: Brazil. "Brasilia meridionalis", s.d., *F. Sellow s.n.* (lectotipo, aquí designado, BR no visto, BR foto SI!; isotipos, K 00470552!, US no visto).

Verbena chamaedryfolia Juss. f. *strigosa* Chodat, Bull. Herb. Boissier, ser. 2, 2: 818. 1902. *Verbena platensis*

(Spreng.) Schnack & Covas var. *stenodes* Briq., Bull. Herb. Boissier, ser. 2, 4: 1055. 1904, nom. illeg. TIPO: Paraguay. Caraguatay, dec., *E. Hassler 5758* (holotipo, G no visto; isotipos, MPU 011496!, P 00650858!, SI!).

Verbena chamaedryfolia f. *foliosa* Chodat, Bull. Herb. Boissier, ser. 2, 2: 818. 1902. *Verbena platensis* (Spreng.) Schnack & Covas var. *latiuscula* Briq., Bull. Herb. Boissier, ser. 2, 4: 1056. 1904, nom. illeg. superfl. TIPO: Paraguay. Capibary, sep., *E. Hassler 4428* (lectotipo, aquí designado, K 000470722!).

Verbena platensis (Spreng.) Schnack & Covas f. *violacea* Moldenke, Phytologia 3: 176. 1949. TIPO: Uruguay. Soriano, Tala, arroyo grande, 3 oct. 1895, *C. Osten 3195* (holotipo, MVM!).

Sufrútice de 30–40 cm alt., base lignificada, apoyante con ramas floríferas ascendentes, entrenudos de 2.5–3.5 cm. Ramas densamente hirsuto-glandulosas. Hojas sésiles o con pecíolo de 1 mm, lámina de 2–3.5(–6) × 0.5–1(–2) cm, ovadas, angostamente ovadas a lineares, enteras, margen revoluto, crenado a lobado, ápice agudo, base cuneada, superficie adaxial rugosa, estrigosa, superficie abaxial híspido-glandulosa, más densamente sobre las venas prominente. Inflorescencia en pleiobotrio con paracladios frondosos que sobrepasan la florescencia principal. Florescencias en espigas cortas, densas, multifloras, raquis alargado, 10–12(–14) cm, en la fructificación; entrenudo basal de 10–70 mm; brácteas de 4.5–7 mm, lineares a angostamente ovadas, superficie adaxial híspido-glandulosa, margen ciliado. Flores con cáliz de 10–17 mm, hirsuto-glanduloso, dientes triangulares, subiguales; corola 18–25 mm, glandulosa en la parte superior externa, blanca, al envejecer rosada, fauce pubescente; par superior de estambres sin apéndices conectivales; estilo de 21–22 mm. Clusa de 4–4.5 mm, recto, ápice obtuso con base no angostada y con repliegue basal interno.

Iconografía. Troncoso y Botta (1993: fig. 45K–O); Botta (1993: 27, fig. 7M–Q), sub *Glandularia platensis*.

Nombre vulgar. Flor de piedra, verbena blanca, en el ejemplar *Muñoz 1379* (SI).

Usos y parte usada. Antiperiódico (de utilidad contra la fiebre recurrente palúdia), anti-ictérico, febrífugo: hoja y flor (Barboza et al., 2006).

Distribución geográfica y hábitat. Glandularia platensis está ampliamente distribuida en el norte, noreste, noroeste y centro de Argentina, también se halla en Bolivia, Brasil y Uruguay. Crece en terrenos pedregosos, bordes de caminos, campos abiertos con afloramientos rocosos, praderas arenosas, cerros, suelos arcillosos, entre los 100 y los 2200 m.

Observaciones. El holotipo de *Verbena platensis* (Sprengel, 1825: 748) "*Ad. Fl. Plata, Sellow*", depositado en B, actualmente se encuentra destruido, y dado que no se han hallado isotipos provenientes de las proximidades del Río de La Plata, se designa como neotipo el ejemplar depositado en P, por tener claramente representados los caracteres que definen la especie y ser de una región próxima a la citada. En el protólogo de *V. teucrioides*, el autor cita material coleccionado por Gillies de Uspallata y Cerro de Portezuelos, localidades de la zona montañosa de Mendoza, Argentina. Sólo se ha podido encontrar el material indicado, que puede corresponderse al citado por el autor y que morfológicamente se corresponde con la descripción original, por lo que se eligió como lectotipo. El holotipo de *V. scordioides*, depositado en B, también está destruido, pero se encontró un ejemplar, sintipo, en BR al que se lo designa como lectotipo ya que se corresponde perfectamente con el protólogo. Con respecto a las variedades establecidas por Chodat, las características de ambas, se corresponde con la variabilidad de la especie. En ambos casos el autor funda las variedades bajo el epíteto *V. chamaedryfolia*, y con posterioridad funda nuevas variedades dentro de *V. platensis*, estableciendo nuevos nombres para las variedades y citando el mismo material tipo, por lo que estos segundos nombres son nombres ilegítimos.

Moldenke (1949b) funda una forma, en base al color de la corola, carácter que es variable con la madurez floral, por lo cual se sinonimiza. A su vez el mismo autor da una combinación en 1974: *Verbena platensis* f. *iverana* (Bosse ex Voss) Moldenke [≡ *V. teucrioides* f. *iverana* Bosse ex Voss], en la descripción original se citan también flores rosadas, y además no se cita material de referencia, por lo que se considera que es un nombre inválido, por lo tanto también lo es la combinación hecha por Moldenke.

Material adicional examinado. ARGENTINA. **Buenos Aires:** Pdo. Adolfo Alsina, Carhué, F.C.S., *Burkart 4799* (SI); Pdo. Bahía Blanca, Bahía Blanca camino a Médanos, 46 km al W de Bahía Blanca, *Bacigalupo 25747* (SI); Pdo. Balcarce, Sierra de La Pelegrina, camino de Mar del Plata a Balcarce, *Correa s.n. BAA2388* (BAA, SI); Pdo. Capital Federal, Madero a Juan J. Passo, *Burkart 19168* (SI); Pdo. Cnel. Suárez, Cerro de la Cruz, *Burkart 28194* (SI); Pdo. Gral. Pinto, Gral. Pinto, *Hicken s.n.* (SI); Pdo. Guaminí, Guaminí, *Hicken s.n.* (SI 3443); Pdo. Junín, Agustina, *Cabrera 6570* (LP); Pdo. Olavarría, Sierras Bayas, *Hunziker, J. H. 11504* (SI); Pdo. Cnel. Pringles, Paso Piedras, *Villamil 2585* (SI); Pdo. Saavedra, Sierra de Curandal, *Fabris 4874* (LP); Pdo. Tandil, Cerro de La Movediza, *Abbiatti 4314* (LP); Pdo. Tornquist, Sierra de la Ventana, *Hicken 78* (SI); Pdo. Trenque-Lauquén, s. loc., s.d., *Cabrera 19458* (SI). **Catamarca:** Dpto. Ambato, La Rinconada, 9 km S de Los Varela, *Saravia Toledo 12899* (CTES); Dpto. Andalgalá, *Jörgensen 1297* (SI). **Córdoba:** Dpto. Calamuchita, Embalse

del Río Tercero, *Krapovickas 6428* (SI); Dpto. Colón, ruta nac. 9, 10 km al N de Jesús María, *Volponi 360* (LP); Dpto. Pocho, subida W de la Sierra de Pocho, *Cabrera 29638* (SI); Dpto. Punilla, Capilla del Monte, *Nicora s.n.* (SI 18625); Dpto. Río Cuarto, ruta prov. 1, 6 km W de Achiras, *Krapovickas 47561* (CTES, SI); Dpto. Río Seco, San Miguel, Río Seco, *Sayago 409* (SI); Dpto. Sta. María, Alta Gracia, *Millán 665* (SI). **Entre Ríos:** Dpto. La Paz, Santa Elena, barrancas, *Burkart 28830* (SI); Dpto. Paraná, ruta 126, Km 110, *Muñoz 1379* (SI). **Jujuy:** Dpto. Doctor Manual Belgrano, entre El Carmen y San Antonio, *Cabrera 34561* (SI); Dpto. El Carmen, Perico, Río Perico, *Krapovickas 17516* (CTES, SI); Dpto. Sta. Bárbara, de El Fuerte a Cachipunco, *Rotman 856* (CTES, SI). **La Pampa:** Dpto. Caleu-Caleu, Anzoátegui, Km 825, vías, *Burkart 15838* (SI); Dpto. Guatraché, Perú, 7 km al S, *Kaufmann 4954* (SI); Dpto. Lihuel Calel, ruta nac. 152 de Lihuel Calel, *Boelcke 16003* (SI); Dpto. Rancul, entre Chamaico y Casimiro Gómez, *Cabrera 19402* (LP). **La Rioja:** Dpto. Gral. Á. Vnte. Peñaloza, Sierra de Los Llanos, subiendo desde Tama hacia Santa Cruz (sector llamado Sierra de Los Quinteros), *Biurrum 6557* (SI); Dpto. Gral. Belgrano, entre Olta y La Chimenea, 20 km al W de la primera, a través de la Sierra de Los Llanos, *Biurrum 6350* (SI); Dpto. Gral. Ocampo, Sierra de Los Llanos, entre los parajes El Quemado y Las Cortaderas, *Biurrum 6242* (SI). **Salta:** Dpto. Guachipas, Cuesta del Lajar, ruta 9, 23 km al SE de Guachipas, *Novara 9403* (SI); Dpto. La Caldera, La Caldera, ruta nac. 9, 16 km al N de Salta, *Burkart 30570* (LP); Dpto. La Candelaria, sierra de Castillejo, *Schreiter 6620* (CONC 133191); Dpto. Rosario de Lerma, Campo Quijano, *Burkart 13206* (SI). **San Juan:** Dpto. Valle Fértil, Sierra de Valle Fértil, Los Bretes, *Kiesling 4993* (SI). **San Luis:** Dpto. Ayacucho, Santa Rosa, Quebrada de la Higuerita, *Burkart 13969* (SI); Dpto. Cnel. Pringles, Potrerillo de Pacanta, esquina del río Grande, *Pastore 2006* (SI); Dpto. La Capital, Cerro Varela, Quebrada La Chilca, *Anderson 1912* (SI). **Tucumán:** Dpto. Burruyacú, 3 km pasando la finca Los Chorrillos, *Galetto 144* (SI). BOLIVIA. **Santa Cruz de la Sierra:** s. loc., *Hicken 21* (SI). BRASIL. **Rio Grande do Sul:** Alegrete, Río Ibirapuitá, *Arbo 2429* (CTES). URUGUAY. **Colonia:** Riachuelo, *Cabrera 3852* (LP). **Florida:** Santa Clara, *Osten 19188* (SI). **Montevideo:** Pajas Blancas, *Rosengurtt 2133* (SI). **Paysandú:** betw. Tambores & Piedra Sola, *Pedersen 15658* (CTES). **Salto:** Cuchilla de Araranguá, along rte. 31, betw. Km 160 from Salto & Los Orientales, *Pedersen 16228* (CTES). **Soriano:** Est. F. C. Juan Jackson, junto al arroyo Grande, Ea. Santa Elena, *Rosengurtt 1009* (SI). **Tacuarembó:** ruta 5, Km 257, *Seijo 2672* (SI).

22. Glandularia radicata (Moldenke) Tronc. ex Múlgura, Monogr. Syst. Bot. Missouri Bot. Gard. 74: 1246. 1999. Basiónimo: *Verbena radicata* Moldenke, Phytologia 9: 184. 1963. Nombre reemplazado para *Verbena radicans* Gillies & Hook., Bot. Misc. 1: 170. 1829 [1830], nom. illeg., non *Verbena radicans* Moench, Methodus (Moench), 369. 1794. *Glandularia radicans* (Gillies & Hook.) Schnack & Covas, Darwiniana 6: 475. 1944, nom. illeg. TIPO: Argentina. [Mendoza:] El Portillo, "In convallibus Andinum prope Mendozam, 7000 ad 8000 ped.", 3 Nov. 1824, *C. B. Gillies s.n.* (holotipo, K 470711 no visto, K foto SI!; isotipo, SI 3824!). Figura 7.

Hemicriptófito rastrero muy ramificado. Ramas jóvenes pubérulas, el resto glabras; entrenudos de 0.8–1.5 cm. Hojas con pecíolo de 4–7 mm, lámina de 0.7–1.5 × 0.5–12 cm, contorno triangular, 3- ó 5-sectas, bipinnatipartidas, subcarnosas, superficies escasamente estrigosas a glabras, lóbulos oblongo-lineares, a veces lobados. Inflorescencia en pleiobotrios, paracladios frondosos mayores que la florescencia principal, que pueden volver a dividirse; entrenudo basal de 1.5–2.5 cm; brácteas de 2 mm, angostamente ovadas, ápice agudo, superficies glabras o subglabras, margen ciliado. Flores con cáliz de 6.5–8.5 mm, estrigoso a híspido, sobre las costillas, dientes triangulares, menores a 1 mm; corola de 12–14 mm, externamente glabra, fauce pubescente; par superior de estambres con apéndices conectivales mayores que las tecas, apenas asomados en la garganta corolar; estilo de 10 mm. Clusas de 3.5–4 mm, el ápice redondeado, la base con repliegue basal y transversal de la pared comisural, superficie externa reticulada, superficie interna papilosa o lisa.

Distribución geográfica y hábitat. *Glandularia radicata* habita en el noroeste de Argentina. Crece en campos secos, laderas, bordes de caminos, entre los 500 y los 3400 m.

Observaciones. *Glandularia radicata* es una especie muy similar a *G. aurantiaca*; se diferencia porque la última se caracteriza por el hábito erecto, hojas y brácteas de mayor tamaño (3–4 mm vs. ca. 2 mm en *G. radicata*) y par superior de estambres con apéndices conectivales inclusos y menores que las tecas.

Material adicional examinado. ARGENTINA. **Catamarca:** Dpto. Andalgalá, Capillitas, *Ruíz Leal 21343* (SI). **Córdoba:** Dpto. San Alberto, Pampa de Achala, *Ruíz Leal 26329* (SI). **La Rioja:** Dpto. Famatina, entre Los Corrales y Cueva de Perez, *Cabrera 27208* (SI). **Mendoza:** Dpto. San Carlos, camino a Laguna Diamante, *Boelcke 4073* (SI). **Salta:** Dpto. San Carlos, Quebrada del Churqui, ca. Amblayo, *Hunziker 2568* (SI). **San Luis:** Sin dpto., Puerta de Pancanta, *Pastore 2035* (SI). **Tucumán:** Dpto. Tafí del Valle, Abra del Infiernillo, *Cabrera 30849* (SI).

23. Glandularia scrobiculata (Griseb.) Tronc., Darwiniana 19: 738. 1975. Basiónimo: *Verbena scrobiculata* Griseb., Abh. Konigl. Ges. Wiss. Gottingen 24: 275. 1879. TIPO: Argentina. Jujuy: San Lorenzo, oct. 1873, *Hieronymus y Lorenz 244* (holotipo, GOET 00187 no visto, GOET foto SI!; isotipo, CORD!, CORD foto SI!).

Verbena hunzikeri Moldenke, Phytologia 2: 321–322. 1947. TIPO: Argentina. Tucumán: entre Alto del Clavillo y

Alpachiri, 1800 m, 20 sep. 1946, *A. T. Hunziker 6812* (holotipo, NY 138275!, NY foto SI!; isotipo, LIL 001700!, SI 3786!).

Verbena moricolor Moldenke, Phytologia 2: 424. 1948. *Glandularia moricolor* (Moldenke) Tronc., Darwiniana 18: 319. 1974. TIPO: Argentina. Jujuy: Ledesma, Sierra de Calilegua, 800 m, 11 oct. 1927, *S. Venturi 5397* (holotipo, CAS 4922 no visto; isotipos, BM 798318!, LIL 1438!, NY 138295 no visto, NY foto SI!, S no visto, S foto SI!, SI 3784!, US 118716!).

Sufrútice de 50–100 cm de alto, ramificada desde la base. Tallos cuadrangulares, escasamente híspido con algunos tricomas glandulares; entrenudos de 5–12 cm. Hojas con pecíolo de 1.5–2.5 cm, lámina de 4–6.5 × 1.5–4 cm, triangulares, enteras, ápice agudo a atenuado, base truncada a obtusa, margen serrado o crenado, a veces hacia la base la incisión de la lámina es más marcada hasta trilobada, superficie adaxial estrigosa, superficie abaxial híspida, principalmente sobre los nervios. Inflorescencia en pleiobotrios heterotéticos. Florescencias en espigas densas, multifloras, raquis alargado en la fructificación; entrenudo basal de 3–4.5 cm; brácteas de 3.5–6 mm, angostamente ovadas, ápice agudo, margen ciliado, superficie abaxial glabra o con escasos tricomas. Flores cáliz de 6.5–8 mm, híspido-glanduloso, dientes desiguales, triangulares, de 0.5–1 mm; corola de 11–12 mm, externamente pubescente, fauce pubescente, lilas o violetas; par superior de estambres con apéndices conectivales poco desarrollados no superando las tecas; estilo de 10–11 mm. Clusas de 2.8–3 mm, ápice redondeado, base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa reticulada, superficie interna papilosa.

Iconografía. Troncoso y Botta (1993: 104, fig. 46), sub *Glandularia scrobiculata.*

Distribución geográfica y hábitat. Glandularia scrobiculata habita en el norte de Argentina y sur de Bolivia. Crece en margen de selvas o borde de caminos, entre los 250 y los 2000 m.

Observaciones. Glandularia scrobiculata es una especie similar a *G. hassleriana* por el hábito, y la pubescencia de los tallos; ambas especies se diferencian, porque *G. hassleriana* tiene la forma elíptica a ovada de las hojas (vs. triangulares en *G. scrobiculata*), el tamaño mayor de las brácteas (9–10.5 mm vs. 3.5–6 mm) y clusas (4–5 mm vs. 2.8–3 mm), éstas de ápice rostrado y par superior de estambres sin apéndices conectivales. Además *G. hassleriana* se distribuye en el noreste de Argentina y en el sur de Brasil, Paraguay y Uruguay (vs. norte de Argentina y sur de Bolivia en *G. scrobiculata*).

Material adicional examinado. ARGENTINA. **Catamarca:** Sin dpto., *Jörgensen, P. 1298* (SI). **Chaco:** Dpto. 1° de Mayo, Colonia Benítez, *Schulz 3988* (CTES). **Jujuy:** Dpto. Ledesma, Parque Nac. Calilegua, *Seijo 1132* (SI); Dpto. Valle Grande, Camino a Valle Grande, *Cabrera 34058* (SI). **Salta:** Dpto. Orán, El Culto, en borde de camino, *Saravia Toledo 14622* (CTES); Dpto. Gral. J. de San Martín, Tartagal, *Meyer 926* (SI); Dpto. Rivadavia, ruta prov. 132, 29 km del desvío de la ruta nac. 50, camino a Santa María, pasando 6 km la Finca Totó, *Morrone 3429* (SI); Dpto. Sta. Victoria, Serranía Finca Arazayal sobre ayo. Arazayal, afluente del Bermejo, 19 km NW de Aguas Blancas, *Arbo 9017* (CTES). **Tucumán:** Dpto. Chicligasta, camino a Andalgalá, poco antes del límite interprov. "La Banderita" Cuesta del Clavillo, *Galetto 222* (SI). BOLIVIA. **Tarija:** Arce, 29.2 km S of Emoroza–Sidras Rd. on rd. to Bermejo, 12.7 km S of Naranjo Agrio, *Solomon 9996* (CTES).

24. Glandularia selloi (Spreng.) Tronc., Darwiniana 13(2–4): 481. 1964. Basiónimo: *Verbena selloi* Spreng., Syst. Veg. (ed. 16) [Sprengel] 2: 750. 1825. *Shuttleworthia selloi* (Spreng.) Walp., Repert. Bot. Syst. [Walpers] 4: 13. 1845. TIPO: Brazil, s. loc., s.d., *F. Sellow s.n. ex Herb. Imperial du Brésil 549* (lectotipo, aquí designado, P 650862!; isotipo, SI!).

Hemicriptófito rastrero, radicante en la mayoría de los nudos, ramas floríferas erguidas. Tallos glabros o con pubescencia híspida retrorsa; entrenudos de 0.5–2 cm, alargándose hacia el ápice de las ramas. Hojas con pecíolo de 3.5–5 mm, lámina de 0.7–2 × 0.5–1.5 cm, 3-sectas, bipinnatipartidas, contorno triangular a ovado, superficie adaxial glabra o escasamente estrigosa, superficie abaxial con pubescencia estrigosa sólo en el nervio medio prominente, lóbulos angostamente ovados de ápice agudo, margen revoluto. Inflorescencia en pleiobotrio heterotético o monobotrio. Florescencias en espigas densas, multifloras, raquis algo alargado en la fructificación; entrenudo basal de 5–15 mm; brácteas de 4–5 mm, angostamente ovadas, ápice subulado, margen densamente ciliado, superficie glabra con pubescencia híspida sobre la vena media. Flores con cáliz de 7–8 mm, híspido, dientes subiguales aristados; corola de 15 mm, externamente pubescente, fauce pubescente, lóbulos emarginados; par superior de estambres con apéndices conectivales cilíndricos, superando las tecas, a veces sobrepasando la corola; estilo de 8–10 mm. Cáliz fructífero contorto hacia el ápice; clusas de 3 mm, cilíndricas, ápice redondeado, base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa reticulada.

Iconografía. Troncoso (1964: 483, fig. 6), sub *Glandularia selloi.*

Distribución geográfica y hábitat. *Glandularia selloi* ha sido colectada en Argentina en la provincia de Entre Ríos; también habita en el sur de Brasil y está ampliamente distribuida en Uruguay. Crece en playas, dunas costeras, praderas marítimas, bordes de caminos y médanos.

Observaciones. En la descripción original, el autor cita material de "Montevideo, Sellow", como hasta el presente, el material hallado de Sellow es de Rio Grande do Sul, se lo elige como lectotipo. Este material se corresponde con el protólogo. *Glandularia selloi* es una especie similar a *G. parodii* por la pubescencia híspida del cáliz, tamaño de las clusas y los apéndices conectivales generalmente sobresaliendo de la garganta corolar; se diferencian ambas especies, porque *G. parodii* tiene los lóbulos filiformes de la lámina foliar con superficie adaxial híspida y el ápice apiculado de las clusas.

Material adicional examinado. ARGENTINA. **Entre Ríos:** Dpto. Concordia, Obraje Salto Grande, *Cabrera 28090* (SI). BRASIL. **Rio Grande do Sul:** Coxilho Piedras Altas, *Pedersen 11445* (CTES, SI). URUGUAY. **Canelones:** Bañados de Carrasco, Arroyo Tropa Vieja, El Pinar, *Krapovickas 16298* (CTES, SI). **Cerro Largo:** Ea. Palleros, *Gallinal 1433* (SI). **Lavalleja:** Minas, Arroyo Aguas Blancas, *Crespo s.n.* (SI 26458). **Maldonado:** Piriápolis, *Lichtenstein s.n.* (SI). **Paysandú:** Alrededores de la ciudad, *Felippone 3249* (SI). **Rocha:** Parque Santa Teresa, *Burkart 21553* (SI). **San José:** Río Santa Lucía, ca. 25 de Agosto, *Rosengurtt B-182* (SI).

25. Glandularia sessilis (Cham.) Tronc., Fl. Il. Entre Ríos 6: 247. 1979. Basiónimo: *Verbena stellarioides* var. *sessilis* Cham., Linnaea 7: 265. 1832. *Verbena sessilis* (Cham.) Kuntze, Rev. Gen. Pl. 3(2): 257. 1898. TIPO: Brazil. s. loc., s.d., *F. Sellow 1563* (lectotipo, aquí designado, G!; isotipo, SI!).

Verbena kuhlmannii Moldenke, Phytologia 31: 29. 1975, syn. nov. TIPO: Brasil. São Paulo: Lake Mojí-Guaqú, Reserve Florestal (Faz. Campininha), 27 oct. 1955, *M. Kuhlmann 3717* (holotipo, US 118708!; isotipo, SI!).

Verbena morongii Britton, Ann. New York Acad. Sci. 7: 192. 1892. TIPO: Paraguay. Central: s. loc., 21 ene. 1889, *Caballero 600* (holotipo, NY 138296 no visto, NY foto SI!; isotipos, PH 28760 no visto, SI!, US 0018717!).

Hemicriptófito erecto de 40–80 cm de alto, apoyante, entrenudos de 3.5–12 cm. Ramas cuadrangulares, tallos glabros o estrigosos hacia el ápice. Hojas sésiles, lámina de 4–7.5(–10) × 0.5–1.3 cm, lineares, angostamente ovadas a ovadas, glabras o escasamente estrigosas, enteras, margen liso o serrado, base truncada a veces cordada. Inflorescencia en monobotrio o pleiobotrio con 1 ó 2 pares de paracladios frondosos que sobrepasan la florescencia principal, pudiendo estar ramificados dando paracladios de segundo orden. Florescencias en espigas densas, multifloras, raquis alargado en la fructificación; entrenudo basal de 20–40 mm; brácteas de 6–8 mm, angostamente ovadas, ápice aristado, iguales a la longitud del cáliz, ciliada en el margen, superficies glabras o estrigosas sobre la vena media. Flores con cáliz de 6–8 mm, híspido sobre las costillas, dientes hasta de 1–1.5 mm; corola de 12.5–13 mm, morada, violácea, pubescente exteriormente, fauce pilosa; par superior de estambres con apéndices conectivales que no superan las anteras; estilo de 11 mm. Clusas de 3 mm, ápice redondeado, base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa reticulada, superficie interna lisa o papilosa.

Iconografía. Troncoso (1979: 249, fig. 114), sub *Glandularia sessilis*.

Distribución geográfica y hábitat. *Glandularia sessilis* habita en el noreste de Argentina, también en Paraguay y Uruguay. Crece en pajonales, inundados, pastizales húmedos y terrenos anegados.

Observaciones. El holotipo de *Verbena sessilis* var. *sessilis*, depositado en B, está actualmente destruido, motivo por el cual se elige como lectotipo el ejemplar del Herbario De Candolle, en G, por corresponderse exactamente con el protólogo. *Verbena kuhlmannii*, fue considerado como sinónimo de *Glandularia stellarioides* (Cham.) Schnack & Covas por Troncoso (1979), pero en el fototipo se ve claramente que la base de las hojas no son decurrentes, sino truncadas, por lo tanto aquí se la sinonimiza con *G. sessilis*.

Pese a que el tipo fue colectado en Brasil, no se ha visto material de dicho país en ninguno de los herbarios consultados.

Especie muy similar a *Glandularia stellarioides*, ésta se diferencia por la base decurrente de las hojas y el tamaño mayor de las brácteas (10–14 mm vs. 6–8 mm en *G. sessilis*).

Material adicional examinado. ARGENTINA. **Chaco:** Dpto. 1° de Mayo, Colonia Benítez, *Schulz 8802* (CTES). **Corrientes:** Dpto. Alvear, 4 km NE de Alvear, ruta nac. 40, Ea. Santa Ana, *Ahumada 3095* (CTES); Dpto. Berón de Astrada, Valencia, 6 km S Yahapé y 3 km S ruta nac. 12, *Carnevalli 5794* (CTES); Dpto. Concepción, Ea. "San Juan Poriajhu", ruta nac. 17, 18 km ruta 12, Potrero Santa Rosa, *Tressens 4211* (CTES, SI); Dpto. Curuzú Cuatiá, Ea. Las Palmas, Bajos del Mocoretá, *Fernández 1068* (CTES); Dpto. Ituzaingó, 17 km NW de San Carlos, Ea. Rincón Chico, *Tressens 3126* (CTES); Dpto. Mercedes, Ea. Iberá, La Flecha S.A., ruta nac. 40, 28 km SE de Colonia Pellegrini, *Schinini 35058* (CTES); Dpto. Sto. Tomé, Rí Aguapey y ruta nac. 14, *Quarín 2642* (CTES). **Entre Ríos:** Dpto. Concordia, arroyo Ayuí, *Burkart 1005* (SI); Dpto. Federación, al N de Laguna Mocoretá, *Burkart 29452* (SI).

Formosa: Dpto. Laishi, Ea. El Bagual de Alparamis S.A. Colonia Presidente Irigoyen, 25 km W de San Francisco de Laishi, *Digiacomo 51* (CTES); Dpto. Patiño, 6 km de San Carlos por ruta, Gral. Belgrano–San Carlos, en dirección S, *Fortunato 2408* (SI); Dpto. Pilcomayo, Ea. "Bouvier", desembocadura del riacho Negro en riacho Monte Claro, *Guaglianone 421* (SI). PARAGUAY. **Alto Paraguay:** Puerto Risso, *Schulz 8835* (CTES). **Caazapá:** Bañado de Yatay-mí, ruta 6, 8 km SW de Yuty, *Schinini 28329* (CTES). **Guairá:** s. loc., *Jörgensen 3773* (SI). **Itapúa:** Ea. "San Miguelito", *Pedersen 4262* (SI). **Paraguarí:** s. loc., *Zardini 16149* (SI). URUGUAY. **Cerro Largo:** s. loc., *Rosengurtt 2351* (SI). **Río Negro:** s. loc., *Rosengurtt 491* (SI).

26. Glandularia stellarioides (Cham.) Schnack & Covas, Bol. Soc. Argent. Bot. 1: 284. 1946. Basiónimo: *Verbena stellarioides* Cham., Linnaea 7: 264. 1832. TIPO: Brasil. *F. Sellow s.n.* (lectotipo, aquí designado, HAL 0098274 no visto [imagen digital!]).

Verbena stellarioides Cham. var. *decurrens* Cham., Linnaea 7: 265. 1832, nom. inval.

Hemicriptófito de 40–70 cm alt., ramas glabras cuadrangulares, escasamente híspidas o escabrosas sobre las costillas; entrenudos 20–35 mm. Hojas sésiles, lámina de 2.5–10 × 0.5–0.6 cm, linear a angostamente ovadas, enteras, superficie adaxial glabra o levemente escabrosa, superficie abaxial glabra o escabrosa sobre la vena media prominente, el resto glabra, margen liso o levemente serrado, escabroso, ápice agudo, base decurrente. Inflorescencia en monobotrio o pleiobotrio con 1 ó 2 pares de paracladios frondosos que sobrepasan la florescencia principal, pudiendo estar ramificados dando paracladios de segundo orden. Florescencias en espigas densas, multifloras, raquis alargado en la fructificación; entrenudo basal de 10–30 mm; brácteas de 10–14 mm con margen ciliado, superficies glabras, ápice aristado, lineare a angostamente ovadas. Flores con cáliz de 8.5–10 mm, dientes hasta 2 mm; corola de 15 mm, pubescente exteriormente, fauce pubescente; par superior de estambres con apéndices conectivales no superando las tecas, inclusos en la garganta corolar; estilo de 12 mm. Clusas de 3–3.5 mm, redondeadas en el ápice, base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa reticulada.

Distribución geográfica y hábitat. Glandularia stellarioides se distribuye en el noreste de Argentina, y en Brasil, en el estado de Rio Grande do Sul. Habita pajonales y pastizales inundables a nivel del mar.

Observaciones. En el prótologo, Chamisso establece dos variedades para la especie, *Verbena stellarioides* var. *decurrens* Cham. y *V. stellarioides* var. *sessilis* esta última considerada actualmente como una especie válida (*Glanduria sessilis*), por lo tanto para el taxón restante, el nombre correcto es *V. stellarioides* (*G. stellarioides*), y *V. stellarioides* var. *decurrens*, debe considerarse un nombre inválido (Greuter et al., 2002, Art. 26.3, Ej. 7). Los materiales originales depositados en B, están destruidos, y se localizó un isotipo en el herbario HAL, del material citado por Chamisso, elegido en esta oportunidad como lectotipo.

Glandularia stellarioides es una especie similar a *G. sessilis*, por las hojas enteras y lineares y apéndices glandulares, cuanto a la base de las hojas y ver observaciones bajo la última especie.

Material adicional examinado. ARGENTINA. **Chaco:** Dpto. 1° de Mayo, Colonia Benítez, *Schulz 1468* (CTES). **Corrientes:** Dpto. Ituzaingó, Ea. San Miguelito, 20 km NE Playadito, *Carnevalli 4967* (CTES); Dpto. Santo Tomé, Ea. "Garruchos", potrero Puente, *Krapovickas 21609* (CTES, SI). **Misiones:** Dpto. Apóstoles, ruta 14, 10 km al N de San José, *Guaglianone 904* (SI); Dpto. Candelaria, Loreto, *Montes 11207* (CTES); Dpto. Eldorado, Eldorado, *Montes 15449* (SI). BRASIL. **Rio Grande do Sul:** Tupanciretan, Chacara, *Rambo 9950* (LIL).

27. Glandularia subincana Tronc., Darwiniana 13(2–4): 478. 1964. TIPO: Uruguay. Salto, Río Arapey, Ao. Valentín, 28 ene. 1937, *B. Rosengurtt B-992* (holotipo, SI 3810!).

Hemicriptófito erecto, sufruticoso en la base, con tallos extendidos, rastreros o radicantes en la base, luego erguidos; ramas subtetrágonas con pubescencia híspida a cano-hispídula, más densa hacia el ápice dándole un aspecto blanquecino; entrenudos de 10–30 mm, más largos hacia el extremo de las ramas. Hojas sésiles o con pecíolo de 5 mm, lámina de 10–30(–45) mm, 2-sectas, de contorno oval-triangular, lóbulos oblongo a angostamente ovados, enteros, dentados o lobados, el ápice subagudo u obtuso, la base atenuada, cara adaxial hirsuta con pequeñas glándulas pateliformes, cara abaxial densamente hirsuta, sobre los nervios, margen revoluto. Inflorescencia en pleiobotrios con 1 ó 2 pares de paracladios frondosos que sobrepasan la florescencia principal. Florescencias en espigas densas, multifloras, raquis alargado en la fructificación; entrenudo basal de 2–5 cm; brácteas de 4–5 mm, angostamente ovadas, subcóncavas en la base, nervio medio manifiesto, incano-hispídulo y con pequeñas glándulas pateliformes. Flores con cáliz de 8–8.5 mm, cano-hispídulo en toda su superficie, más densamente en la mitad inferior y con pelitos más rígidos y oblicuos hacia el ápice de las costillas y los dientes, y con glándulas pateliformes; dientes hasta de 1 mm,

desiguales, subulados; corola de 12–15 mm, violácea, morada o lila azulada, glabra exteriormente, fauce pubescente; par superior de estambres con apéndices conectivales superando las tecas y asomando en la garganta corolar; estilo de 8.5–9 mm. Clusas de 2.5–2.8 mm, el ápice redondeado, la base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa alveolada en la mitad superior, el resto surcado, la superficie interna blanco-verrucosa.

Iconografía. Troncoso (1964: 480, fig. 5), sub *Glandularia subincana*.

Distribución geográfica y hábitat. Glandularia subincana habita en el este de Argentina y en Uruguay; crece en laderas sobre suelos arenosos, desde el nivel del mar hasta los 350 m.

Observaciones. Glandularia subincana es afín a *G. selloi*, ambas se diferencian, porque *G. selloi* tiene hábito rastrero, cáliz con pubescencia híspida, dientes aristados y por la corola pubescente externamente. También es afín a *G. tenera*, diferenciándose, la última, por el hábito rastrero y el ápice de las clusas rostrado.

Material adicional examinado. ARGENTINA. **Buenos Aires:** Pdo. Cnel. Suárez, Campo La Susanita, a 10 km de la Estación Peralta, *Ruíz Huidobro 1176* (SI); Pdo. Gral. Pueyrredón, Ea. La Brava, en camino lateral frente a la Laguna, *Rúgolo 832* (SI); Pdo. Tandil, s. loc., *Cabrera 20852* (SI); Pdo. Tornquist, Sierra de la Ventana, *Rentzell 1099* (SI). **Corrientes:** Dpto. Ituzaingó, 31 km desde Posadas hacia Corrientes por la ruta 73-25, *Schnack s.n.* (SI 26411); Dpto. Mercedes, 3 km N de ruta nac. 123, *Cáceres 17* (CTES). **Entre Ríos:** Dpto. La Paz, ruta nac. 126 a Paraná, 10 km al S de La Paz, *Burkart 30111* (SI); Dpto. Uruguay, Concepción del Uruguay, *Troncoso 2641* (SI). **La Pampa:** Dpto. Maracó, Gral. Pico, *Burkart 9932* (SI). **Misiones:** Sin dpto., Puente Pampa, *Kermes 3 BAB 6568* (SI). **San Luis:** Dpto. Gobernador Dupuy, entre Nueva Galia y Arizona, *Guiñazú p.p. 226* (SI). **Santa Fé:** Dpto. Vera, próximo desvío Cerritos, *Pensiero 1547* (SI). URUGUAY. **Artigas:** s. loc., *Marchesi 10045* (SI). **Paysandú:** ruta 26, camino de Paysandú a Tacuarembó, ca. 120 km de Paysandú, *Morrone 5255* (SI). **Soriano:** Juan Jackson, Ea. Santa Elena, *Gallinal 492* (SI).

28. Glandularia sulphurea (D. Don) Schnack & Covas, Darwiniana 6: 475. 1944. Basiónimo: *Verbena sulphurea* D. Don, Brit. Fl. Gard. [Sweet] 6 (ser. 2, 3): tab. 221. 1835. *Shuttleworthia sulphurea* (D. Don) Meisn., Pl. Vasc. Gen. 2: 198. 1840. *Uwarowia sulphurea* (D. Don) Schauer, Prodr. [DC.] 11: 551. 1847. TIPO: Chile. Región V: prope Valparaíso, 1831, *H. Cuming 450* (holotipo, K 00470708 no visto, K foto SI!).

Sufrútice procumbente o ascendente, muchas veces con rizoma bien desarrollado, ramificado. Hojas con lámina 3-partida a 3-secta, segmentos lineares de 1 mm lat., ápice agudo, margen algo revoluto. Inflorescencia en pleiobotrios o monobotrios. Florescencias en espigas densas, globosas, multifloras, raquis alargado en la fructificación; brácteas lineares a angostamente ovadas, acuminadas; cáliz con dientes agudos; corola cremosa, amarilla, blanca, glabra exteriormente, fauce pubescente; lóbulos bilobados, emarginados; par superior de estambres con apéndices conectivales superando la longitud de las tecas y sobresaliendo de la garganta corolar, negruzcos. Cáliz fructífero de ápice contorto; clusas cilíndricas, el ápice obtuso, la base no angostada, superficie dorsal, reticulada, superficie ventral papilosa, base no angostada y con repliegue basal y transversal de la pared comisural.

Clave para Diferenciar las Variedades de *Glandularia sulphurea*

28a. Ramas híspidas; brácteas de 3–3.5 mm long.; cáliz de 7–8 mm long.; corola de 16–18 mm de largo..... 28a. var. *sulphurea*
28b. Ramas híspido-glandulares; brácteas de 4–6.5 mm long.; cáliz de 5.5–6 mm long.; corola de 13 mm de largo ..... 28b. var. *pedunculata*

28a. Glandularia sulphurea var. **sulphurea**. Figura 8.

Verbena sulphurea D. Don var. *fuscorubra* Skottsb., Acta Horti Göthob. 18: 15. 1950. TIPO: Chile. Coquimbo: Loma de Fray Jorge, 19 ago. 1917, *Skottsberg 885* (holotipo, GB no visto, GB foto SI!; isotipos, NY no visto, NY foto SI!, S no visto, S foto SI!).

Verbena sulphurea D. Don var. *scabra* Acevedo, Bol. Mus. Hist. Nat. 25: 67–68. 1951. TIPO: Chile. Atacama: Huayco, Set. 1885, *s. coll. s.n.* (holotipo, SGO 54741! [código de barras SGO 4284], SGO 54741 foto SI!; isotipo, SI!).

Sufrútice de 20–25 cm alt., procumbente o ascendente, muchas veces con rizoma bien desarrollado, ramificado; ramas híspidas de base leñosa. Hojas con pecíolo de 3–5 mm, lámina de 10–20 × 7–11 mm, 3-partida a 3-secta, segmentos lineares de 1 mm lat., ápice agudo, superficies adaxial y abaxial híspidas con algunos tricomas glandulares, margen algo revoluto. Inflorescencia generalmente en monobotrios. Florescencias en espigas densas, globosas, multifloras, raquis alargado en la fructificación; entrenudo basal de 10–25 mm; brácteas de 3–3.5 mm, angostamente ovadas, acuminadas, híspido-glandulosas. Flores con cáliz de 7–8 mm, híspido-glanduloso, dientes de 0.5–1 mm, triangulares; corola de 16–18 mm, cremosa, amarilla, blanca, glabra exteriormente, fauce pubescente; lóbulos bilobados,

emarginados; par superior de estambres con apéndices conectivales superando la longitud de las tecas y sobresaliendo de la garganta corolar, negruzcos; estilo de 13–14 mm. Cáliz fructífero de ápice contorto; clusa de 3.5 mm, cilíndricas, el ápice obtuso, la base no angostada, cara externa pardo oscura, reticulada, cara comisural papilosa, base no angostada y con repliegue basal y transversal de la pared comisural.

Distribución geográfica y hábitat. *Glandularia sulphurea* var. *sulphurea* habita en Argentina en las provincias de San Juan y Mendoza y en la Región III, IV y V de Chile. Crece en suelos arenosos de alta cordillera, entre los 2600 y los 3300 m.

Observaciones. El holotipo de *Glandularia sulphurea* var. *sulphurea* se cultivó a partir de semillas enviadas por Cuming a Don. En la descripción original no se hace mención a los apéndices glandulares, pero éstos están claramente dibujados en la lámina. *Verbena sulphurea* D. Don f. *alba* Moldenke (Moldenke, 1949b) fue publicado como un nomen nudum.

Glandularia sulphurea var. *intermedia* (Kuntze) L. E. Navas es considerada en el presente trabajo como sinónimo de *G. macrosperma*, ver el tratamiento bajo esta última especie.

Glandularia sulphurea var. *sulphurea* es una especie muy similar a *G. microphylla*, ver observaciones bajo la última especie.

Material adicional examinado. ARGENTINA. **La Rioja:** Sin dpto., entre Coa Tocino y Portillo, *Krapovickas 5408* (SI). **Mendoza:** Dpto. Las Heras, Altos de Los Manantiales, *Ruíz Leal 23619* (SI); Dpto. Malargüe, Distrito Río Grande, Carta "El Manzano", Pampa Palanco, inmediaciones del campamento de Y.P.F., *Ambrosetti 30877* (SI); Dpto. San Carlos, betw. Militar Gral. Alvarado & ruta 40, *Böcher 2070* (SI); Dpto. San Rafael, Río Diamante, *Carette 39* (SI). **San Juan:** Dpto. Angaco, Sierra de Pie de Palo, Mogote de los Corralitos, *Kiesling 6314* (SI); Dpto. Calingasta, El Pachón, Los Erizos, *Kiesling 1360* (SI). CHILE. **Región III:** Huasco, Atacama, Lomas frente a Las Losas, *Ricardi 3939* (CONC 24056). **Región IV:** Limari, Coquimbo, Ovalle, Fray Jorge, *Jiles 3459* (CONC 41700). **Región V:** Petorca, Zapallar, *Hartwig s.n.* (CONC 11552).

28b. Glandularia sulphurea var. **pedunculata** (Gay) L. E. Navas, Fl. Cuenca de Santiago de Chile 3: 69. 1979. Basiónimo: *Verbena sulphurea* D. Don var. *pedunculata* Gay, Fl. Chil. 5: 8. 1849. TIPO: Chile. Santiago, 1837, *C. Gay s.n.* (lectotipo, aquí designado, SGO 54748! [código de barras SGO 4283], SGO foto SI!; isotipos, P no visto, G no visto, SI!).

Verbena sulphurea D. Don var. *alba* Moldenke, Phytologia 11: 247. 1965. TIPO: Chile. Coquimbo: Est. Fray Jorge, 215 m, 13/14 ago. 1917, *C. J. F. Skottsberg & I. Skottsberg 739* (holotipo, GB no visto, GB foto SI!; isotipos, NY 00138330 no visto, NY foto SI!, S no visto, S foto SI!).

Observaciones. En el protólogo de la variedad, se citan varios materiales, se eligió el mencionado por que se corresponde con la descripción original. Es una especie endémica de las Regiones IV, V y VI de Chile, por lo tanto excede a los objetivos planteados para este tratamiento.

29. Glandularia tenera (Spreng.) Cabrera, Man. Fl. Alrededores Buenos Aires 398. 1953. Basiónimo: *Verbena tenera* Spreng., Syst. Veg. (ed. 16) [Sprengel] 2: 752. 1825. *Shuttleworthia tenera* (Spreng.) Walp., Repert. Bot. Syst. [Walpers] 4: 14. 1845. TIPO: Brazil. *F. Sellow s.n.* (lectotipo, aquí designado, K 470522!; isotipos, E 00373267!, K 00470523!).

Verbena tenera Spreng. var. *albiflora* Kuntze, Revis. Gen. Pl. 3: 258. 1898. *Verbena tenera* Spreng. f. *albiflora* (Kuntze) Moldenke, Phytologia 41: 451. 1979. TIPO: Argentina. Santa Fe: Ceres, oct. 1892, *C. E. O. Kuntze s.n.* (holotipo, NY 00138335 no visto, NY foto SI!; isotipos, F 0074535 no visto, LP!).

Verbena pulchella Sweet, Brit. Fl. Gard. [Sweet] (ser. 1) 3, tab. 295. 1827–1829, non *Verbena pulchella* Greene, Pittonia 5: 136. 1903, syn. nov. *Shuttleworthia pulchella* (Spreng.) Meisn., Pl. Vasc. Gen. [Meisner], 2: 198. 1840. *Glandularia pulchella* (Sweet) Tronc., Darwiniana 13: 473. 1964. TIPO: Sweet, Brit. Fl. Gard. [Sweet] (ser. 1) 3, tab. 295. 1827–1829.

Glandularia pulchella (Sweet) Tronc. var. *clavellata* Tronc., Darwiniana 13: 476, fig. 3. 1964, syn. nov. *Verbena pulchella* Sweet var. *clavellata* (Tronc.) Shinners, Sida 3: 266. 1966. TIPO: Argentina. Buenos Aires: Sierra de la Ventana, parque prov., 6 oct. 1939, *A. L. Cabrera 5288* (holotipo, SI 3783!).

Glandularia pulchella (Sweet) Tronc. var. *gracilior* Tronc., Darwiniana 13: 476. 1964, syn. nov. *Verbena pulchella* Sweet var. *gracilior* (Tronc.) Shinners, Sida 2(3): 266. 1966. TIPO: Argentina. Buenos Aires: Pdo. Gral. Madariaga, Villa Gesell, 5 mar. 1961, *A. Burkart 22380* (holotipo, SI!; isotipo, US 118729 no visto).

Verbena santiaguensis (Covas & Schnack) Moldenke f. *albiflora* Moldenke, Phytologia 18: 295. 1969, syn. nov. TIPO: Argentina. Buenos Aires: Pdo. Gral. Pueyrredón, Playa Grande, 10 dic. 1944, *J. M. Villegas Vaquero 666* (holotipo, NY 00138321 no visto; isotipos, BR no visto, LIL no visto, NY no visto, SI!).

Hemicriptófito rastrero, sufruticoso en la base, rastrero, tallos extendidos, ramas floríferas ascendentes, glabras o escasamente estrigosas; ramas subtetrágonas, entrenudos de 0.8–6 cm, estrigoso-pubescentes a veces hirsútulas. Hojas con pecíolo de 5–10 mm, lámina de 1.5–2 × ca. 1.5 cm, de contorno oval-triangular, 3- ó 5-sectadas, bipinnatipartidas a bipinnatisectas, superficies estrigosas con pequeñas glándulas pateliformes en la cara abaxial, base

atenuada, ápice subagudo, segmentos lineares a angostamente ovados de 3–7 × ca. 1 mm, margen entero, revoluto o no. Inflorescencias en pleiobotrio heterotético paniculados o en monobotrios, por reducción de la zona de enriquecimiento. Florescencias en espigas multifloras, raquis algo alargado en la fructificación; entrenudo basal de 15–20 mm; brácteas de 3.5–4.5 mm, oval-angostamente ovadas, nervio medio prominente, subcóncavas en la base, estrigosas y con glándulas pateliformes; cáliz 8–9 mm, densamente estrigoso con glándulas pateliformes subsésiles, dientes tubulados, abaxiales de 1 mm, conniventes en la fructificación; corola de 12–13 mm, glabra exteriormente, fauce pubescente, violácea; par superior de estambres con apéndices conectivales cilíndricos, delgados, superando la longitud de las tecas, brevemente exertos; estilo de 8–11 mm. Clusas de 4–6 mm, cilíndricos, ápice rostrado, base no angostada y con repliegue basal y transversal de la pared comisural cara dorsal pardo oscura, superficie externa reticulada, superficie interna papilosa.

Iconografía. Troncoso (1964: 472, fig. 1); Troncoso (1979: 257, fig. 120), sub *Glandularia tenera*.

Nombre vulgar. Margarita en el ejemplar *Bowes, N. D. 46* (SI); margarita morada, verbena americana, yerba meona.

Distribución geográfica y hábitat. Glandularia tenera habita en el norte y centro de Argentina y en el sur de Brasil y Uruguay. Crece en campos arenosos y abiertos, orillas de caminos, terrenos altos, bordes de arroyos y ríos, terrenos pedregosos, entre el nivel del mar y los 560 m.

Observaciones. El tipo de *Verbena tenera*, *Sello s.n.*, fue depositado en B y está actualmente destruido, razón por la cual se elige como lectotipo uno de los isotipos depositado en K por corresponderse exactamente con el protólogo.

Se sinonimizan los siguientes taxones, *Glandularia pulchella* (Sweet) Tronc., *G. pulchella* var. *clavellata*, *G. pulchella* var. *graciolor* y *Verbena santiaguensis* f. *albiflora*, porque al estudiar los respectivos materiales tipo no pudieron hallarse características que permitiesen su diferenciación, sumando además, que presentan una distribución geográfica similar.

Especie muy similar a *Glandularia aristigera*, ver observaciones bajo esta especie.

Material adicional examinado. ARGENTINA. **Buenos Aires:** Capital Federal, terrenos ca. Chacarita, *Hicken s.n.* (SI 3373); Pdo. Adolfo Alsina, Lago Epecuen, *Cabrera 8058* (SI); Pdo. Avellaneda, s. loc., *Burkart 698* (SI); Pdo. Bahía Bca., de Bahía Bca. a Médanos, *Burkart 25638* (SI); Pdo. Balcarce, Bosch, *Nicora 2014* (SI); Pdo. Baradero, Baradero, alto de la barranca, *Burkart 8490* (SI); Pdo. Campana, Otamendi ca. Campana, *Burkart 23908* (SI); Pdo. Carlos Casares, Bellocq, *Cabrera 9850* (SI); Pdo. Chascomús, s. loc., *Ezcurra 6* (SI); Pdo. Cnel. Rosales, Puerto Belgrano, *Hicken s.n.* (SI 3374); Pdo. Cnel. Suárez, Campo "La Susana" a 10 km de Estación Peralta, *Ruiz Huidobro 1176* (SI); Pdo. Gral. Alvarado, Miramar, *Troncoso s.n.* (SI 17859); Pdo. Villa Gesell, Villa Gesell, *Burkart 22380* (SI); Pdo. Gral. Pinto, Gral. Pinto, *Hicken s.n.* (SI 3369); Pdo. Gral. Pueyrredón, Mar Chiquita, *Ruíz Leal 22276* (SI); Pdo. La Plata, Vivero Belgrano, frente al club Gimnacia y Esgrima, *Hicken s.n.* (SI 27709); Pdo. Luján, Luján, *Nicora 138* (SI); Pdo. Verónica, Verónica, alrededores, *Guaglianone 1314* (SI); Pdo. Monte, Monte, *Burkart 19015* (SI); Pdo. Necochea, Necochea, *Hicken s.n.* (SI 3367); Pdo. Olavarría, R 226, al S de Olavarría, *Burkart 28965* (SI); Pdo. Olivos, Barrancas de Olivos, *Hicken s.n.* (SI 1407); Pdo. Ramallo, s. loc., *Burkart 12748* (SI); Pdo. Rivadavia, Fortín Olavarría, *Cabrera 14780* (SI); Pdo. Saladillo, Cazón, *Fabris 344* (SI); Pdo. San Isidro, San Isidro, calle Centenario, *Burkart s.n.* (SI 27708); Pdo. San Martín, Villa Pogreso, entre las vías del tranvía eléctrico a San Martín, *Hicken s.n.* (SI 3372); Pdo. San Miguel, Saliendo hacia San Miguel, *Villamil 4348* (SI); Pdo. San Nicolás, San Nicolás, barrancas, *Cabrera 7195* (SI); Pdo. Tandil, Sierra de las Ánimas, Cerro de la Cascada, *Morrone 5492* (SI); Pdo. Tornquist, Sierra de la Ventana, *Dawson 13* (SI); Pdo. Tres Arroyo, Claromecó, *Burkart 18149* (SI); Pdo. Tres de Febrero, Santos Lugares F.C.R., *Guglialmelli s.n.* (SI 27712); Pdo. Vicente López, La Lucila, *Hicken s.n.* (SI 27711); Pdo. Villarino, Médanos, *Villamil 7131* (SI); Pdo. Zárate, Lima, barrancas del río Paraná de las Palmas, *Cabrera 27626* (SI). **Chaco:** Dpto. 1° de Mayo, Colonia Benítez, *Spegazzini s.n.* (BAF); Dpto. Mayor Fontana, Benítez, *Meyer 142* (SI); Dpto. San Fernando, Trayecto camino a Resistencia, *Meyer 141a* (SI). **Córdoba:** Dpto. Ascochinga, s. loc., *Giardelli 223* (SI); Dpto. Calamuchita, Villa Gral. M. Belgrano, alrededores de la ciudad, *Morrone 5783* (SI); Dpto. Colón, La Granja, *Troncoso 291* (SI); Dpto. Punilla, La Falda, camino a la Cascada de Olaen, *Botta 294* (SI); Dpto. Río Cuarto, Camino de Holmberg a Malena, *Troncoso 6022* (SI); Dpto. Roque Saenz Peña, 20 km antes de Laboulaye, *Cabrera 29520* (SI); Dpto. San Alberto, Santa Catalina, *Giardelli s.n.* (SI 14923); Dpto. Tercero Arriba, Hernando, *Krapovickas 6403* (SI). **Corrientes:** Dpto. Bella Vista, Bella Vista, *Cocucci 3066* (SI); Dpto. Capital, Corrientes, Pericón, *Schinini 11600* (SI); Dpto. Concepción, Paraje Rincón de Luna entre Batel y Batelito, Estancia Los Tres Rincones, Potrero Alto-Cué, *Cano 513* (SI); Dpto. Curuzú Cuatiá, Curuzú-Cuatiá, ruta 127, *Burkart 28822* (SI); Dpto. Esquina, 77 km de Goya camino a Esquina, ruta nac. 12 y Río Corrientes, *Morrone 5354* (SI); Dpto. Goya, 8 km S de Goya, ruta prov. 27, *Krapovickas 17824* (SI); Dpto. Itatí, ruta nac. 12, 6 km de Itatí, *Schinini 4476* (SI); Dpto. Ituzaingó, Isla Apipé Grande, río Paraná, brazo San José, Destacamento Vizcaíno, *Guaglianone 224* (SI); Dpto. Lavalle, Cañada de Los Perros, ruta prov. 27, S de Santa Lucía, *Schinini 5143* (SI); Dpto. Mercedes, 3 km SW del empalme de la ruta nac. 14 con la ruta nac. 119, próximo a la estación San Dionisio, *Correa 5268* (SI); Dpto. Monte Caceros, ruta nac. 14 entre Mocoretá y Cuatro Bocas, *Cabrera 27656* (CTES, SI); Dpto. Paso de los Libres, ruta prov. 23, entre empalme con ruta nac. 129 y cruce del río Miriñay, *Correa 5227* (SI); Dpto. San Cosme, Paso de la Patria, *Krapovickas 15588* (SI); Dpto. San Luis del Palmar, 19.5 km SE de San Luis del Palmar, *Schinini 31286* (SI); Dpto. San Martín, 20 km de Yapeyú hacia Santo Tomé,

Zuloaga 3120 (SI); Dpto. Sauce, Río Guayquiraró, 18 km S de Sauce, *Cristóbal 1619* (SI). **Entre Ríos:** Dpto. Colón, Arroyo El Pelado, 68 km al S de Ubajay, *Burkart 23466* (SI); Dpto. Concordia, Concordia a Federal, ruta prov. 128, Km 515, *Burkart 28821* (SI); Dpto. Diamante, ca. Puiggari, arroyo La Ensenada, *Guaglianone 183* (SI); Dpto. Federación, río Uruguay, *Burkart 27338* (SI); Dpto. Feliciano, Feliciano, *Martínez Crovetto 6107* (SI); Dpto. Gualeguay, a Puerto Ruiz, *Burkart 24230* (SI); Dpto. Gualeguaychú, ruta nac. 12, después de Ceibas camino a Perdices, *Troncoso 2207* (SI); Dpto. Islas del Ibicuy, ruta nac. 12, 3 km de Celbas camino a Médanos, *Morrone 5209* (SI); Dpto. La Paz, Paso Yunque, *Burkart 27052* (SI); Dpto. Paraná, Villa Urquiza, *Antuña 68* (SI); Dpto. Uruguay, ruta prov. 39, entre Caseros y Herrera, *Bacigalupo 591* (SI); Dpto. Victoria, s. loc., *Burkart 8678* (SI). **La Pampa:** Dpto. Capital, ruta nac. 5, 10 km E de Santa Rosa, *Corea 8786* (SI); Dpto. Chalileo, ruta nac. 143, 120 km al W de Telsen, *Cano 3024* (SI); Dpto. Guatraché, Ea. La Julia, *Rúgolo 1268* (SI); Dpto. Maracó, Gral. Pico, *Burkart 9791* (SI); Dpto. Santa Rosa, s. loc., *Steibel 1059* (SI). **Misiones:** Dpto. Capital, ruta prov. 105, arroyo Piedras, *Zuloaga 2321* (SI). **San Luis:** Dpto. La Capital, Chosme, Alto Pencoso, *Sayago 2511* (SI). **Santa Fé:** Dpto. 9 de Julio, 3 km N de Tostado, *Pensiero 3366* (SI); Dpto. Caseros, Los Nogales, *Pastore 1163* (SI); Dpto. Castellanos, Rafaela, *Raviolo 7* (SI); Dpto. Garay, ruta prov. 1, Santa Rosa de Calchines, *Deginani 1837* (SI); Dpto. Gral. Obligado, Reconquista, *Alonso 370* (SI); Dpto. La Capital, Barrancas de Rosario, *Gómez s.n.* (SI 3368); Dpto. San Cristobal, entre Ceres y Colonia Alpina, *Vegetti 1006* (SI); Dpto. San Jerónimo, Coronda, arroyo Matadero, ruta nac. 11, *Krapovickas 17805* (SI). **Santiago del Estero:** Dpto. Rivadavia, 2 km al N de Selva sobre ruta nac. 34, *Tivano 644* (SI). BRASIL. **Santa Catarina:** Araranguá, *Reitz c1280e* (SI). PARAGUAY. **Itapúa:** Yacyreta, Yacyreta dam island reserve, Oculto, Palm savanna, *Zardini 59482* (SI). URUGUAY. **Artigas:** Río Uruguay y arroyo Itacumbú, *Rosengurtt 10484* (SI). **Colonia:** Nueva Palmira, Río Uruguay, Nueva Palmira, Río Uruguay, *Morrone 5224* (SI). **Paysandú:** ruta 3, Km 484, *Del Puerto 11325* (SI). **Soriano:** Playa de la Agraciada, *Izaguirre 11887* (SI).

30. Glandularia tomophylla (Briq.) P. Peralta, Darwiniana 45: 241. 2007. Basiónimo: *Verbena tomophylla* Briq., Bull. Herb. Boissier, ser. 2, 4: 1061. 1904. TIPO: Paraguay. Caraguatay, oct. 1898/99, *E. Hassler 3295* (holotipo, G no visto; isotipos, G foto SI!, K 470721 no visto, K foto SI!, P no visto, SI 3828!, SI 3829!). Figura 9.

Glandularia spectabilis (Moldenke) Botta, Hickenia 2(28): 128. 1995, syn. nov. Basiónimo: *Verbena spectabilis* Moldenke, Phytologia 2: 426. 1948. TIPO: Argentina. Misiones: Posadas, Loreto, "Magdalena", 6 Feb. 1908, *E. L. Ekman 1980* (holotipo, NY 13325 no visto; isotipos, NY foto SI!, S no visto, S foto SI!, SI 3821!).

Verbena megapotamica (Spreng.) Cabrera & G. Dawson f. *pinnatiloba* Kuntze, Revis. Gen. Pl. 3(2): 256. 1898. Basiónimo: *Verbena pinnatiloba* (Kuntze) Moldenke, Phytologia 2: 28. 1941. TIPO: Paraguay: s. loc., Sep. 1892, *E. O. Kuntze s.n.* (holotipo, NY 138392 no visto; isotipos, NY foto SI!, SI!).

Verbena ramboi Moldenke, Phytologia 3: 427. 1951, syn. nov. TIPO: Brasil. Rio Grande do Sul: Faz. Sta. Cecilia, pres. S. Gabriel, 15 ene. 1944, *B. Rambo 25787* (holotipo, PACA no visto; isotipos, NY 00138315 no visto, NY foto SI!, SI!).

Verbena calliantha Briq., Bull. Herb. Boissier, ser. 2, 4: 1059. 1904, syn. nov. TIPO: Paraguay. Concepción, in dumetis, Oct., *E. Hassler 7615* (lectotipo, aquí designado, NY 138249!, NY foto SI!; isotipo, BM 98802 no visto).

Verbena calliantha Briq. var. *microsoma* Briq., Bull. Herb. Boissier, ser. 2, 4: 1060. 1904, syn. nov. TIPO: Paraguay. Cerro Pyta, Oct., *E. Hassler 1272* (holotipo, G!).

Verbena storeoclada Briq., Bull. Herb. Boissier, ser. 2, 4: 1060. 1904, syn. nov. TIPO: Paraguay. Iter ad Yerables, sierra de Maracayú, in regiorne fluminis Corrientes, Set., *E. Hassler 4489* (holotipo, G no visto; isotipos, K!, K foto SI!, F 0074534 no visto [imagen digital!], F foto SI!, MPU 011503 no visto [imagen digital!], NY 0138327 no visto [imagen digital!], P 00650864 no visto [imagen digital!], P0065865 no visto [imagen digital!], GH no visto, UC 935083 no visto [imagen digital!], SI!).

Hemicriptófito rastrero de 50–100 cm, ramificado desde la base, ramas floríferas ascendentes, pubescencia híspida a estrigosa y retrorsa; entrenudos de 2.5–6 cm. Hojas con pecíolo de 5–7 mm, lámina de 3–5 × 0.8–2.5 cm, contorno ovadas, ápice agudo, base acuminada, 2/3 superior lobado, 1/3 basal sectado, lóbulos lobados, superficie adaxial estrigosa, superficie abaxial híspida. Inflorescencia en pleiobotrio heterotético o monobotrio. Florescencias en espigas densas, multifloras, raquis alargado en la fructificación; entrenudo basal de 15–30 mm; brácteas de 3–5 mm, angostamente ovadas, superficie abaxial estrigosa, a veces con tricomas glandulares pateliformes, margen ciliado; cáliz de 8–10 mm, estrigoso a híspido con tricomas glandulares pateliformes, dientes del cáliz filiformes hasta 1.8 mm; corola de 12–12.5 mm, purpúreas, lilas, pubescente exteriormente, fauce pubescente; par superior de estambres con apéndices conectivales apenas mayores que las tecas, inclusos; estilo de 10–10.5 mm. Clusas de 2.5–3.5 mm, ápice redondeado, base no angostada y con repliegue basal y transversal de la pared comisural, superficie externa reticulada hacia el ápice, hacia la base acanalada, superficie interna papilosa.

Nombre vulgar. Margarita, ejemplar *Montes 12539* (SI).

Distribución geográfica y hábitat. Glandularia tomophylla habita en el este y centro de Argentina y también en Paraguay y en el estado de Rio Grande do Sul en Brasil. Crece en campos de altura con afloramientos rocosos, selva marginal, bordes de caminos, suelos arenosos, desde el nivel del mar hasta los 650 m.

Observaciones. Al estudiar el tipo de *Verbena spectabilis*, se vio que las características del ejemplar no concordaban con la descripción original. En dicha descripción (Moldenke, 1948a: 426) hace mención al no alargamiento de la inflorescencia: "...aparentemente no elongada después de la antesis...", pero pudo confirmarse que el raquis se alarga en la fructificación. Por otra parte, las restantes características que describen a dicha especie coinciden con las de *Glandularia tomophylla*, razón por la cual se las considera sinónimos en este tratamiento.

Se llevan, además, a la sinonimia las especies *V. ramboi*, *V. calliantha*, *V. calliantha* var. *microsoma* y *V. storeoclada*, hemos tenido oportunidad de estudiar el material tipo de estos taxones y los mismos se corresponden con *G. tomophylla*, como así también la distribución geográfica y la descripción original de los mismos.

Material adicional examinado. ARGENTINA. **Chaco:** Dpto. San Fernando, Casa Lata, campo ribereño, río Paraguay, *Rojas 11785* (SI). **Córdoba:** Dpto. Calamuchita, Rincón de Luna, *Pedersen 4484* (CTES, SI). **Corrientes:** Dpto. Berón de Astrada, 15 km W de Itá Ibaté, Ayo. Santa Isabel, *Schinini 14102* (CTES, SI); Dpto. Capital, ruta nac. 12, 14 km de Itá-Ibaté, hacia Corrientes, *Zuloaga 3308* (SI); Dpto. Concepción, Rincón de San Pedro, *Burkart 31069* (SI); Dpto. Gral. Paz, Capillitas, *Pedersen 12388* (CTES, SI); Dpto. Goya, Balsa del Río Santa Lucía, *Guaglianone 221* (SI); Dpto. Ituzaingó, Isla Apipé Chico, *Schinini 15480* (CTES, SI); Dpto. Mburucuyá, Ea. Sta Teresa, *Krapovickas 13641* (CTES); Dpto. Saladas, 23 km E de Saladas, *Quarín 3881* (CTES, SI); Dpto. San Miguel, 12 km S de Caa-Catí, ruta nac. 5, *Ahumada 1768* (CTES); Dpto. San Roque, Ea. "San Antonio", ca. 30 km al NE de Chavaría, camino a Concepción, 4 km al E de la ruta, al E del casco, *Arbo 7048* (CTES); Dpto. Santo Tomé, Estancia "Garruchos", *Pedersen 9134* (SI). **Entre Ríos:** Dpto. Concordia, Obraje Salto Grande, *Cabrera 28090* (SI). **Formosa:** Dpto. Pilcomayo, Colonia Palma Sola, R 86, finca de Marcelina Cáceres de Galeano, *Schinini 31321* (CTES). **Misiones:** Dpto. Apóstoles, ruta prov. 2, de Azara a Tres Capones, 4 km de Azara, *Zuloaga 8103* (SI); Dpto. Candelaria, Loreto, *Burkart 15226* (SI); Dpto. Concepción, Estancia de Elsa Prates, sobre el Río Uruguay, *Biganzoli 1729* (SI); Dpto. Leandro N. Além, Entrada a Paso Carreta, sobre ruta nac. 14, *Krapovickas 14985* (CTES); Dpto. San Ignacio, 15 km E de ruta nac. 12, prox. Ayo. Las Dunas, *Keller 418* (CTES); Dpto. San Javier, Cerro del Monje, 6 km NE de San Javier, *Arbo 5895* (CTES). BRASIL. **Rio Grande do Sul:** Cachoeira do Sul, *Sobral 1718* (SI). PARAGUAY. **Alto Paraná:** Ñacunday, *Montes 10913* (SI). **Caaguazú:** a 20 km de Caaguazú hacia Yhú, *Brescia 5075* (SI). **Central:** s. loc., *Rojas 5891* (SI). **Guairá:** s. loc., *Montes 12539* (SI). **Itapúa:** Arroyo San Rafael, ruta 1, 15 km SE de Gral. Delgado, *Arbo 1974* (CTES, SI). **Misiones:** Ea. La Soledad, 3 km S de Santiago, *Schinini 26070* (CTES). **Ñeembucú:** Destacamento Naranjito, río Paraguay, *Schulz 7989* (CTES). **Paraguarí:** Parque Nac. Ybycuí, Cerrado vegetation near rd. to César Barrientos, *Zardini 7486* (SI).

31. Glandularia tristachya (Tronc. & Burkart) Schnack & Covas, Bol. Soc. Argent. Bot. 1: 284. 1946. Basiónimo: *Verbena tristachya* Tronc. & Burkart, Darwiniana 7: 208, fig. 1–3. 1946. TIPO: Argentina. Entre Ríos: Dpto. Ibicuy, Delta superior, Isla de las Lechiguanas, 30 dic. 1945, *A. Burkart 15644* (holotipo, SI 3798!; isotipos, K 470705!, K 470704!, NY 128343! NY foto SI!, SI 3799!, SI 3800!, US 118741!).

Hierba perenne, con ramas glabras; entrenudos hasta 10 cm. Hojas sésiles, lámina de 2.5–5.5 × 0.3–0.5 cm, enteras, lineares a angostamente ovadas, glabras, ápice agudo, base atenuada, margen liso o dentado. Inflorescencias en pleiobotrio heterotético paniculados o en monobotrios. Florescencias en espigas multifloras, densas, raquis algo alargado en la fructificación; entrenudo basal de 8 cm; brácteas de 4–4.5 mm, angostamente ovadas, con escasos pelitos en el margen; cáliz de 5 mm, escasamente estrigoso sobre las costillas; dientes de 0.5 mm, triangulares; corola de 7–7.5 mm, azul-morada, fauce pubescente; par superior de estambres sin apéndices conectivales; estilo de 5–6 mm. Clusas de 4–4.5 mm, ápice obtuso, pared externa reticulada, interna lisa, castaño claro, base no angostada y con repliegue basal y transversal de la pared comisural.

Iconografía. Troncoso (1979: 251, fig. 115), sub *Glandularia tristachya*.

Distribución geográfica y hábitat. *Glandularia tristachya* crece en el este de Argentina, en las provincias de Corrientes y Entre Ríos y en Brasil. Habita generalmente sobre pajonales desde el nivel del mar hasta los 50 m.

Observaciones. *Glandularia tristachya* es similar a *G. sessilis* y *G. stellarioides*, por el hábito herbáceo y las hojas de forma linear a angostamente ovadas y enteras; pueden diferenciarse principalmente por la presencia de apéndices conectivales en *G. stellarioides* y *G. sessilis*, las brácteas de mayor tamaño (6–8 mm en *G. sessilis* y 10–14 mm en *G. stellarioides* vs. 4–4.5 mm en *G. tristachya*) y el menor tamaño de las clusas (3–3.5 mm vs. 4–4.5 mm en *G. tristachya*).

Material adicional examinado. ARGENTINA. **Corrientes:** Dpto. Ituzaingó, Isla Apipé Grande, Puerto Mora, *Krapovickas 24385* (SI); Dpto. San Cosme, Paso de la Patria, *Meyer 2158* (SI). **Entre Ríos:** Dpto. Feliciano, Chalicito, arroyo El Cajón, frente a Curuzú Cutiá, *Burkart 27057* (SI). BRASIL. **São Paulo:** Mojí-Guacú, Reserva Forestal, Fezenda Campininha, *Kuhlmann 3717* (SI).

32. Glandularia tweedieana (Niven ex Hook.) P. Peralta, comb. nov. Basiónimo: *Verbena tweedieana* Niven ex Hook., Bot. Mag. 63 [n.s. 10], tab. 3541. 1836. *Verbena megapotamica* Spreng.

var. *tweedieana* (Niven ex Hook.) Kuntze, Revis. Gen. Pl. 3(2): 256. 1898. TIPO: Uruguay. Laguna de La Molina, s.d., *J. Tweedie s.n.* (holotipo, K no visto, K foto SI!; isotipo, SI 3941!).

Verbena tweedieana Niven ex Hook. var. *arraniana* Niven en Maund & Hensl. ex Maund, Botanist 2: t. 60. 1838, syn. nov. TIPO: tab. 60 en Maund, Botanist 2. 1838 (lectotipo, aquí designado, tab. 60 en Maund, 1838).

Glandularia incisa (Hook.) Tronc. en Cabrera, Colecc. Ci. Inst. Nac. Tecnol. Agropecu. 5a: 135. 1965, syn. nov. Basiónimo: *Verbena incisa* Hook., Bot. Mag., pl. 3628. 1839. TIPO: Argentina. Santa Fe, s.d., *J. Tweedie s.n.* (lectotipo, aquí designado, K 470716!, K foto SI!; isotipo, SI 3942!).

Verbena megapotamica var. *truncatula* Briq., Annuaire Conserv. Jard. Bot. Geneve 5–9: 3. 1904. TIPO: Paraguay, s.d., *B. Balanza 1024c* (holotipo, G no visto, G foto SI!).

Hemicriptófito rastrero, a veces con ramas apoyantes, radicantes en los nudos, cano-pubescentes; entrenudos de 2.5–4 cm. Hojas con pecíolo de 4–7 mm, láminas enteras, basales triangulares-oblongas, de base truncada, margen inciso-lobado; láminas apicales de menor tamaño, ovadas subsésiles, margen inciso-serrado; cano-hispídulas en ambas caras. Inflorescencia en monobotrio o pleiobotrios. Florescencias en espigas multifloras, densas, raquis algo alargado en la fructificación; entrenudo basal de 2.5–3 cm; brácteas de 2.5–3.5 mm, angostamente ovadas; cáliz de 10–11.5 mm, dientes breves, agudos, densamente hispídulo-glandulosos, pubescencia blanquecina; corola de 1.4–1.7 cm, rojo o rosada, fauce pubescente; par superior de estambres sin apéndice conectivales; estilo de 14.5–15.5 mm. Clusas de 4.5–5 mm, rectas, ápice obtuso, base no angostada y con repliegue basal y transversal de la pared comisural.

Iconografía. Troncoso (1979: 248, fig. 113), sub *Glandularia incisa*.

Nombre vulgar. Margarita de campo, en *Vavrek 287* (SI); margarita en *Castañeda Vega 60* (SI).

Distribución geográfica y hábitat. Glandularia tweedieana está ampliamente distribuida en el norte y centro de Argentina, también crece en Bolivia, Brasil, Paraguay y Uruguay. Habita los bordes de caminos, lugares abiertos, suelos arenosos, y margen de selva, desde los 100 m hasta los 2600 m.

Observaciones. Entre los ejemplares citados en el protólogo de *Verbena incisa* Hook., se eligió el ejemplar citado anteriormente, porque se corresponde con la descripción. *Verbena tweedieana* Niven, había sido sinonimizada por Troncoso (1971) bajo *Glandularia megapotamica*. Se estudió uno de los isotipos, y los estambres no presentan apéndice conectival, la corola es roja, la pubescencia es similar a *G. incisa*, tiene dos tipos de hojas basales dentadas superiores incisas y más angostas, y además la inflorescencia se alarga en la fructificación. Estos dos últimos caracteres pueden verse claramente en la fotografía del ejemplar de K en SI. Por lo tanto en la presente revisión se la considera que ambas especies, *G. incisa* y *V. tweedieana*, deben tratarse como una misma especie, además *G. tweedieana* tiene prioridad sobre *G. incisa*, por lo tanto *G. incisa* pasa a la sinonimia y se realiza la nueva combinación *G. tweedieana* (Niven ex Hook.) P. Peralta.

Para *Verbena tweedieana* var. *arraniana* se eligió como tipo la lámina publicada en el protólogo, porque no se ha hallado hasta el presente material de herbario observado por el autor. En la descripción original se indica la transición de este taxón entre *V. tweedieana* y *V. incisa*, de la observación realizada en los materiales de herbario no se pueden establecer límites entre los taxones, por lo cual este taxón se sinonimiza.

Tweedie le envió semillas a Niven al National Botanic Gardens, Glasnevin procedentes de Uruguay. En el protólogo (Hooker, 1836), el autor hace referencia a la similitud que presenta la especie con *Verbena chamaedryfolia*, hoy *Glandularia peruviana*, pero son dos entidades diferentes, ver las observaciones bajo esta última especie.

Material adicional examinado. ARGENTINA. **Buenos Aires:** Pdo. Baradero, s. loc., *Burkart 8474* (SI); Pdo. Gral. Uriburu, Las Palmas, *Boelcke 4860* (SI); Pdo. Ramallo, s. loc., *Burkart 12764* (SI); Pdo. San Nicolás, San Nicolás, barrancas, *Cabrera 7181* (SI); Pdo. San Pedro, San Pedro, *Nicora 3541* (SI); Pdo. Zárate, puerto Terminal Las Palmas, Paraná de las Palmas, Km 123, *Hurrell 5207* (SI). **Catamarca:** Dpto. Andalgalá, s. loc., *Jörgensen 1028* (SI). **Chaco:** Dpto. 1 de Mayo, Colonia Benítez, *Schulz 7440* (CTES); Dpto. Alte. Brown, ruta nac. 16, 21 km W of Concepción del Bermejo, *Soza 1813* (SI); Dpto. Independencia, Campo Largo, 2 km hacia Colonia José Mármol, La Montenegrina, *Martínez 9578* (SI); Dpto. San Fernando, 11 km W de Resistencia, ruta nac. 16, *Urbani 76* (CTES); Dpto. Tapenagá, Enrique Urien, *Rodrigo 2437* (SI). **Córdoba:** Dpto. Calamuchita, entre Los Reartes y Los Molinos, 3–4 km del último puente, *Ruíz Leal 26293* (SI); Dpto. Capilla del Monte, s. loc., *Nicora s.n.* (SI 18560); Dpto. Ischilín, Ongamira, *Fabris 7953* (LP); Dpto. Punilla, Cabalango, *Pensiero 893* (SI); Dpto. San Justo, 13 km E de La Francisca, *Krapovickas 18520* (CTES, SI). **Corrientes:** Dpto. Bella Vista, Bella Vista, *Cabrera 29016* (SI); Dpto. Capital, 5 km E de Laguna Brava, *Krapovickas 15838* (SI); Dpto. Concepción, Paraje Rincón de Luna, entre Batel y Batelito, Ea. "Los Tres Rincones", potrero Alto-Cué, *Cano 490* (SI); Dpto. Curuzú Cuatiá, ruta prov. 126, ca. 50 km W of jct. with ruta nac. 14, *Olmstead 2004-108* (SI); Dpto. Empedrado, El Sombrerito, Estación Experimental del INTA, *Ahumada 78* (CTES, SI); Dpto. Esquina, 25 km S

of Esquina, ruta nac. 12, *Harley 28011* (CTES); Dpto. Itatí, Itatí, orillas del Río Paraná, *Schinini 4449* (CTES); Dpto. Mburucuyá, Ea. Santa Teresa, *Cabrera 27751* (SI); Dpto. Saladas, 17 km E de Saladas, *Quarín 3879* (CTES, SI); Dpto. San Cosme, Paso de La Patria, *Cristóbal 1210* (CTES, SI); Dpto. San Luis del Palmar, ruta prov. 5, 18 km SE de San Luis del Palmar, *Cristóbal 1241* (SI); Dpto. Santo Tomé, Garruchos, Ea. San Juan Bautista, *Krapovickas 25759* (CTES, SI). **Entre Ríos:** Dpto. Concordia, Camino de Villa Federal a La Paz, próximo a Villa Federal, *Burkart 23457* (SI); Dpto. Diamante, Punta Gorda, *Burkart 22280* (CTES, SI); Dpto. Federación, ruta nac. 14, 2 leguas de Chajarí, *Cano 1901* (SI); Dpto. Feliciano, río Guayquiraró, Paso Ocampo, *Burkart 23458* (SI); Dpto. La Paz, Santa Elena, *Burkart 23462* (SI); Dpto. Paraná, s. loc., *Boelcke 1252* (SI); Dpto. Villaguay, 79 km antes de Villaguay, ruta nac. 18, *Naranjo 754* (SI). **Formosa:** Dpto. Formosa, s. loc., *Birabén s.n.* (LP 906985); Dpto. Laishi, Ea. El Bagual de Alparamis S.A. Colonia Presidente Irigoyen, 25 km W de San Francisco de Laishi, *Digiacomo 49* (CTES); Dpto. Matacos, Ing. G. N. Juárez, calles del pueblo, *Arenas 2378* (SI); Dpto. Patiño, 17 km del cruce con ruta nac. 86, por ruta a Cogoik, *Fortunato 2295* (SI); Dpto. Pilcomayo, Parque Nac. Pilcomayo, *Guaglianone 2184* (SI); Dpto. Piraré, ruta nac. 81, Las Mercedes, 28 km NW de Pirané, *Krapovickas 19561* (CTES, SI). **La Pampa:** Dpto. Toay, Bajo de las Palomas, *Steibel 5167* (SI). **La Rioja:** Dpto. Chamical, Sierra de Los Llanos, Quebrada de la Aguadita, *Aguirre 825* (CTES); Dpto. Gral. Belgrano, Sierra de Los Quinteros, paraje "Las Barrancas", 1.5 km N de El Toro Muerto, alrededores del arroyo, *Biurrum 2690* (SI). **Misiones:** Dpto. Apóstoles, San José, Escuela Agrotécnica P. Gentilini, *s. coll. s.n.* (SI); Dpto. Candelaria, Santa Ana, *Rodriguez 576* (SI); Dpto. Capital, ruta a Asunción, a 117 km después de Encarnación, *Maruñak 124* (SI); Dpto. San Ignacio, Ruinas de San Ignacio, *Jov s.n.* (LP 905475); Dpto. San Pedro, s. loc., *s. coll. s.n.* (LP). **Salta:** Dpto. Orán, Río Piedras, *Rodríguez 55* (BAF); Dpto. Rivadavia, entre río Teuco y Los Blancos, *Correa 7582* (SI). **San Luis:** Dpto. Cnel. Pringles, Trapiche, *Dawson 3504* (LP); Dpto. Gral. Pedernera, Mercedes, Camino de Mercedes a La Toma, a 25 km de Mercedes, *Cabrera 25418* (LP); Dpto. La Capital, en las afueras, sobre la rotonda que divide las rutas que van a Trapiche y El Potrero de Los Funes, *Galetto 22* (SI). **Santa Fé:** Dpto. 9 de Julio, 7 km NW de Tostado, *Pensiero 3499* (CTES); Dpto. Gral. Obligado, Mocoví, *Venturi 33* (SI); Dpto. La Capital, Barrancas de Rosario, *Gómez s.n.* (SI 3353); Dpto. Las Colonias, próximo Esperanxa, *Pensiero 1395* (SI); Dpto. San Cristóbal, 5 km NW de Ceres por ruta nac. 95, *Pensiero 2838* (SI); Dpto. San Javier, Colonia Galense, *Ragonese 9* (SI). **Santiago del Estero:** Dpto. Capital, s. loc., *Castañeda Vega 60* (SI); Dpto. La Banda, s. loc., *Maldonado 472* (SI). **Tucumán:** Dpto. Tafí del Valle, s. loc., *Volponi 377* (LP). BOLIVIA. **Chuquisaca:** Luis Calvo, El Salvador, zona central, *Pensiero 4308* (SI). **Santa Cruz de la Sierra:** Cordillera, Boyuibe, *Nee 35333* (SI). **Tarija:** Caingua, 15 km N de Villa Montes, *Krapovickas 19436* (CTES). BRASIL. **Rio Grande do Sul:** Torres, *Reitz 4445* (SI). PARAGUAY. **Alto Paraguay:** Chaco, *Herter 85* (SI). **Boquerón:** Campos Pto. Casado, frente a Puerto Risso, *Schinini 8891* (CTES). **Caaguazú:** Arroyo Cambay, *Zardini 23824* (SI). **Central:** Tavarory, 1 km E of Río Paraguay, *Zardini 24439* (SI). **Cordillera:** Tobati, "Ybytú Silla" mesa, *Zardini 27284* (SI). **Guairá:** Cordillera de Ybytyruzú, rd. to Cantera Jhú, tall forest 2 km S of rte. to Cnel. Oviedo, *Zardini 14586* (SI). **Ñeembucú:** Pilar, *Ramirez 342* (SI). **Paraguarí:** Acahay, cerro Acahay, ca. 5 km from main hwy., near area of rock extration, *Landrum 8627* (CTES). **Presidente Hayes:** betw. pozo colorado & Concepción, *Zardini 58674* (SI). **San Pedro:** Villa Primavera, *Woolston 731* (SI). URUGUAY. **Paysandú:** Camino de Paysandú a Casablanca, *Del Puerto 1626* (SI).

33. Glandularia venturii (Moldenke) Botta, Bol. Soc. Argent. Bot. 26: 246, fig. 2H–P. 1990. Basiónimo: *Verbena venturii* Moldenke, Known Geogr. Distrib. Verb. Avicenn. 79. 1942. TIPO: Argentina. Tucumán: Dpto. Capital, río Salí frente al Duraznito, 600 m, 3 sep. 1920, *S. Venturi 949* (holotipo, NY 138346! NY foto SI!; isotipos, LIL no visto, K 470702!, SI 3812!, SI 3811!, US 118745!).

Verbena arenaria Moldenke, Phytologia 8: 59. 1961. TIPO: Argentina. Tucumán: Dpto. Capital, Río Salí, 450 m, 18 dic. 1923, *S. Venturi 2441* (holotipo, US 118668!; isotipo, SI 3673!).

Glandularia perakii Covas & Schnack, Revista Argent. Agron. 11: 89. 1944, syn. nov. Basiónimo: *Verbena perakii* (Covas & Schnack) Moldenke, Phytologia 2: 149. 1946. TIPO: Argentina. Mendoza: Dpto. Las Heras, Dique Papagallos, 3 dic. 1943, *B. Covas 2110* (holotipo, SI 3809!).

Glandularia glandulifera (Moldenke) Ragonese, Revista Invest. Agric. 5: 206. 1951, syn. nov. Basiónimo: *Verbena glandulifera* Moldenke, Phytologia 3: 44. 1948. TIPO: Argentina. Córdoba: Dpto. Colón, Ascochinga, 700 m, 26 oct. 1936, *N. Troncoso 292* (holotipo, NY 138267!; isotipos, SI 3792!, SI 3793!).

Hierba perenne, procumbente, tallos ascendentes de 30–50 cm alt., ramas híspidas-glandulosas; entrenudos de 1.5–4 mm. Hojas con pecíolos de 0.3–1.5 mm, lámina de 3–4.5 × 2–3.5 mm, lobada, 3-fida o 3-secta, raramente enteras de margen serrado o crenado, contorno ovado, ápice agudo, superficie adaxial estrigosa-glandulosa, superficie abaxial híspida-glandulosa. Inflorescencia en pleiobotrios con 2 pares de paracladios frondosos, que sobrepasan la florescencia principal. Florescencias en espigas densas multifloras, raquis alargado en la fructificación; entrenudo basal de 3–6 mm; bráctea de 3.5–5.5 mm, angostamente ovadas, ápice agudo, margen ciliado, superficie abaxial híspida-glandulosa; cáliz de 6–7 mm, híspido-glanduloso, dientes triangulares de 0.5 mm, subiguales; corola de 13–15 mm, violeta o lila, pubescente exteriormente, fauce pubescente; par superior de estambres con apéndices conectivales, menores a las tecas; estilo de 7–7.5 mm. Clusas de 2.5–3 mm, cilíndricas, ápice obtuso, base no angostada con repliegue basal y transversal de la pared comisural, superficie externa reticulada.

Iconografía. Covas y Schnack (1944: 90, fig. 1), sub *Glandularia perakii*; Botta (1990: 245, fig. 2H–

P), Troncoso y Botta (1993: 112, fig. 50H–P), sub *Glandularia venturii*.

Nombre vulgar. Yerba l'incordio, en *Arenas s.n. CEFAPRIN 278* (SI); primavera en *Kiesling 5004* (SI); yerba de la incordia, en *Biurrum 3609* y *Biurrum 5486* (SI).

Usos. Es usado como remedio para el corazón de acuerdo al ejemplar de *Kiesling 5004* (SI).

Distribución geográfica y hábitat. *Glandularia venturii* crece en el centro y noroeste de Argentina. Habita en suelos arenosos, pedregosos, laderas rocosas, entre los 350 y los 3500 m.

Observaciones. Se estudiaron los materiales tipo de *Glandularia perakii* y *G. glandulifera*, sin poder establecer diferencias en cuanto la pubescencia de toda la planta, morfología de flor y fruto y hábito, motivo por el cual se las considera sinónimos en el presente tratamiento. *Glandularia venturii* se caracteriza por una densa pubescencia híspido-glandulosa en tallos, hojas, brácteas y cálices.

Material adicional examinado. ARGENTINA. **Catamarca:** Dpto. Ambato, Balcones, Sierra de Ambato, *Parodi 14069* (SI); Dpto. Ancasti, entre Ancasti e Icaña, *Troncoso 1791* (SI); Dpto. Andalgalá, s. loc., *Jörgensen 1026* (SI); Dpto. Belén, Cóndor Huasi, *Arenas s.n. CEFAPRIN 278* (CEFAPRIN); Dpto. Capital, El Juncal hacia la quebrada de San Lorenzo, *Ulibarri 916* (SI); Dpto. Capoyán, Cuesta de la Cébila, *Kiesling 5916* (SI); Dpto. Pomán, Campo de Villanca, *Biloni 6169* (SI); Dpto. Tinogasta, Cuesta de Zapata en el camino de Tinogasta a Belén, *Cabrera 16747* (LP, SI). **Córdoba:** Dpto. Calamuchita, Valle de los Reartes, *Castellanos 121* (SI); Dpto. Colón, Quebrada de Las Rocas, camino a La Calera, *Lanfranchi 1070* (SI); Dpto. Gral. San Martín, Cerros de Villa María, *Cabrera 16414* (CTES); Dpto. Ischilín, de Dean Funes a Córdoba, Río Pinto, arroyo, ruta nac. 60, *Troncoso 1921* (SI); Dpto. Pocho, bifurcación camino de Pocho a los Palmaz Tamiza, *Luti 4493* (SI); Dpto. Punilla, alrededores de Copina, *Fabris 1033* (CTES); Dpto. Río Cuarto, Las Peñas, *Bianco-Cantero 1209* (SI); Dpto. Río Seco, Sierra de Villa María, *Cabrera 29672* (SI); Dpto. San Alberto, Mina Clavero, camino a Nono, *Bonzani 95* (SI); Dpto. San Javier, Villa Dolores, Las Tapias, *Burkart 13828* (SI); Dpto. Santa María, autopista Córdoba-Carlos Paz, en el cruce con empalme a Alta Gracia, *Galetto 74* (SI); Dpto. Sobremonte, San Francisco del Chañar, unos 5 km al W del pueblo, camino hacia Caspi, *Múlgura 2928* (SI); Dpto. Unión, San Marcos, *Nicora s.n.* (SI 17785). **Jujuy:** Dpto. Santa Bárbara, El Fuerte, ca. 5 km hacia Abra de los Morteros, *Kiesling 5481* (SI). **La Rioja:** Dpto. Arauco, Sierra de Ambato, Quebrada de la Sebila, *Troncoso 1855* (SI); Dpto. Capital, Puerta de la Quebrada, *Alaín 48* (SI); Dpto. Chamical, Sierra de Los Llanos frente a Chamical, entre El Durazno y Tuisón, a 2 km del primero, *Biurrum 7215* (SI); Dpto. Chilecito, Cuesta de Miranda, *Schnack s.n. SI 26416* (SI); Dpto. Famatina, entre Los Corrales y Cueva de Perez, Cantera de Ocre, *Cabrera 27141* (SI); Dpto. Felipe Varela, Cuesta de Miranda, *Botta 687* (SI); Dpto. Gral. La Madrid, entre Jagué y Salina del Leoncito, a 8 km del cruce con el camino a Chile, Praje llamado Los Mudaderos, *Biurrum 5486* (SI); Dpto. Gral. Ocampo, Sierra de Los Llanos, frente a Catuna, entre los parajes El Quemado y Las Cortaderas, *Biurrum 6240* (CTES); Dpto. Vinchina, dejando la ruta de Jagué a Pircas Negras, rumbo a la Saina del Leoncito, a 12 km del cruce, Playa del Mudadero, *Biurrum 4504* (SI). **Mendoza:** Dpto. Capital, ca. Parque Gral. San Martín, *Hunziker, J. H. 9898* (SI); Dpto. Las Heras, campos de Las Mojaditas, *Ruíz Leal 21899* (SI); Dpto. Luján de Cuyo, *Covas s.n.* (SI). **Salta:** Dpto. Anta, Parque Nac. El Rey, Cerro Chañar, Roquedal, *s. coll. 1648* (SI); Dpto. Cachi, Cachipampa a Tin Tin, *Cabrera 30753* (SI); Dpto. Candelaria, Río del Potrero, *Venturi 3677* (SI). **San Juan:** Dpto. Angaco, Sierra de Pie de Palo, camino al Mogote de Los Corralitos, *Kiesling 4798* (SI); Dpto. Caucete, ruta nac. 141, entre Bermejo y Vallecito, a 16 km de éste, *Biurrum 5405* (CTES); Dpto. Iglesia, entre La Ciénaga e Iglesia, *Cabrera 27008* (SI); Dpto. Jáchal, de Jáchal a Gualamayo, *Tombesi 37* (SI); Dpto. Sarmiento, Quebrada de La Flecha, *Kiesling 4032* (SI); Dpto. Ullún, Hualilan, *Kiesling 7861* (SI); Dpto. Valle Fértil, Quebrada de Mesada, Chucuma, *Múlgura 741* (SI); Dpto. Zonda, Ea. Maradona, Agua Pinto, *Kiesling 6064* (SI). **San Luis:** Dpto. Ayacucho, A 10 km al S de San Francisco del Monte de Oro, *Herrera 370* (SI); Dpto. Belgrano, Estancia El Médano, 65 km al NW de San Luis, *Anderson 3076* (SI); Dpto. Chacabuco, 4 km al S de Papagayos, *Botta 519* (SI); Dpto. Cnel. Pringles, La Carolina, *Seijo 1809* (CTES); Dpto. Gral. Pedernera, ruta nac. 7, Km 706, *Ocampo 1429* (CTES); Dpto. Gdor. Dupuy, ruta nac. 7, entre Mercedes y L. Luna, *Cano 2762* (SI); Dpto. La Capital, ca. cruce de rutas nac. 7 y 147, 715 m, *Anderson 1631* (SI). **Santiago del Estero:** Dpto. Choya, próximo Choya, *Slanis 193* (SI); Dpto. Guasayán, Sierra de Guasayán, Puerta Chiquita, *Rotman 197* (SI); Dpto. Ojo de Agua, Arroyo La Primavera, *Perez Moreau 3687* (CTES); Dpto. Rivadavia, 2 km al N de Selva sobre ruta nac. 34, *Tivano 644* (CTES).

Taxones Excluidos de la Flora Argentina

Los siguientes taxones, *Glandularia marrubioides* (Cham.) Tronc., *G. kuntzeana* (Moldenke) Tronc. y *G. pulchra* (Moldenke) Botta, fueron excluídos de la Flora Argentina ya que no se han registrado citas para dicha región; aquellos ejemplares determinados bajo los nombres anteriormente señalados corresponden a otras especies.

Nombres Dudosos

Verbena peruviana var. *glabriuscula* Kuntze, Revis. Gen. Pl. 3(2): 257. 1898. TIPO: Argentina. Buenos Aires, Sierra de la Ventana, *Hauthal 52*.

No se ha podido localizar hasta ahora el material citado por O. Kuntze, por lo tanto consideramos el mismo como un taxon dudoso.

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Apéndice 1. Índice de nombres científicos. Lista de especies y variedades aceptadas de *Glandularia* J. F. Gmel.

1. *Glandularia andalgalensis* (Moldenke) P. Peralta
2. *Glandularia andina* (Griseb.) P. Peralta
3. *Glandularia araucana* (Phil.) Botta
4. *Glandularia aristigera* (S. Moore) Tronc.

5a. *Glandularia aurantiaca* (Speg.) Botta var. *aurantiaca*
5b. *Glandularia aurantiaca* var. *glabra* (Hicken) P. Peralta

6. *Glandularia cabrerae* (Moldenke) Botta

7. *Glandularia cheitmaniana* (Moldenke) Botta & Poggio
8. *Glandularia dissecta* (Willd. ex Spreng.) Schnack & Covas
9. *Glandularia flava* (Gillies & Hook. ex Hook.) Schnack & Covas
10. *Glandularia guaranitica* Tronc.
11. *Glandularia hassleriana* (Briq.) Tronc.
12. *Glandularia lilloana* (Moldenke) Botta
13. *Glandularia macrosperma* (Speg.) Tronc.
14. *Glandularia megapotamica* (Spreng.) Cabrera & G. Dawson
15. *Glandularia mendocina* (Phil.) Covas & Schnack
16. *Glandularia microphylla* (Kunth) Cabrera
17. *Glandularia nana* (Moldenke) Tronc.
18. *Glandularia parodii* Covas & Schnack
19. *Glandularia peruviana* (L.) Small
20. *Glandularia phlogiflora* (Cham.) Schnack & Covas
21. *Glandularia platensis* (Spreng.) Schnack & Covas
22. *Glandularia radicata* (Moldenke) Tronc. ex Múlgura
23. *Glandularia scrobiculata* (Griseb.) Tronc.
24. *Glandularia selloi* (Spreng.) Tronc.
25. *Glandularia sessilis* (Cham.) Tronc.
26. *Glandularia stellarioides* (Cham.) Schnack & Covas
27. *Glandularia subincana* Tronc.
28a. *Glandularia sulphurea* (D. Don) Schnack & Covas var. *sulphurea*
28b. *Glandularia sulphurea* (D. Don) Schnack & Covas var. *pedunculata* (Gay) L. E. Navas
29. *Glandularia tenera* (Spreng.) Cabrera
30. *Glandularia tomophylla* (Briq.) P. Peralta
31. *Glandularia tristachya* (Tronc. & Burkart) Schnack & Covas
32. *Glandularia tweedieana* (Niven ex Hook.) P. Peralta
33. *Glandularia venturii* (Moldenke) Botta

Apéndice 2. Lista de las especies sinonimizadas en este trabajo con indicación de su ubicación taxonómica actual.

Glandularia aurantiaca (Speg.) Botta var. *glaberrima* (Moldenke) Botta [= *G. aurantiaca* var. *glabra* (Hicken) P. Peralta]
Glandularia glandulifera (Moldenke) Ragonese [= *G. venturii* (Moldenke) Botta]
Glandularia glutinosa (Kuntze) Covas & Schnack [= *G. flava* (Gillies & Hook. ex Hook.) Schnack & Covas]
Glandularia incisa (Hook.) Tronc. [= *G. tweedieana* (Niven ex Hook.) P. Peralta]
Glandularia perakii Covas & Schnack [= *G. venturii* (Moldenke) Botta]
Glandularia pulchella (Sweet) Tronc. [= *G. tenera* (Spreng.) Cabrera]
Glandularia pulchella var. *clavellata* Tronc. [= *G. tenera* (Spreng.) Cabrera]
Glandularia pulchella var. *gracilior* Tronc. [= *G. tenera* (Spreng.) Cabrera]
Glandularia santiaguensis Covas & Schnack [= *G. andina* (Griseb.) P. Peralta]
Glandularia spectabilis (Moldenke) Botta [= *G. tomophylla* (Briq.) P. Peralta]
Glandularia sulphurea var. *intermedia* (Kuntze) L. E. Navas [= *G. macrosperma* (Speg.) Tronc.]
Verbena erinoides var. *andina* Griseb. [= *Glandularia andina* (Griseb.) P. Peralta]
Verbena calliantha Briq. [= *Glandularia tomophylla* (Briq.) P. Peralta]
Verbena calliantha var. *microsoma* Briq. [= *Glandularia tomophylla* (Briq.) P. Peralta]
Verbena hassleriana var. *ovatifolia* Moldenke [= *Glandularia phlogiflora* (Cham.) Schnack & Covas]
Verbena kuhlmannii Moldenke [= *Glandularia sessilis* (Cham.) Tronc.]
Verbena megapotamica Spreng. var. *tweedieana* (Niven ex Hook.) Kuntze [= *Glandularia tweedieana* (Niven ex Hook.) P. Peralta]
Verbena pulchella Sweet f. *latilobata* Moldenke [= *Glandularia dissecta* (Willd. ex Spreng.) Schnack & Covas]
Verbena radicata Moldenke var. *glabra* (Hicken) Moldenke [= *Glandularia aurantiaca* var. *glabra* (Hicken) P. Peralta]
Verbena ramboi Moldenke [= *Glandularia tomophylla* (Briq.) P. Peralta]
Verbena santiaguensis (Covas & Schnack) Moldenke f. *albiflora* Moldenke [= *Glandularia tenera* (Spreng.) Cabrera]
Verbena storeoclada Briq. [= *Glandularia tomophylla* (Briq.) P. Peralta]
Verbena tweedieana Niven ex Hook. [= *Glandularia tweedieana* (Niven ex Hook.) P. Peralta]

Apéndice 3. Índice de colecciones. Cada espécimen es citado por el nombre del primer colector en el caso de que otros coleccionistas participen en la colección. En el caso de no poseer número de colección se indica el número de herbario en que se encuentra depositado o en su defecto sólo el herbario. Se indica entre paréntesis el número de orden de la especie a que corresponde y la sigla de herbario en donde se encuentra depositado el material (véase Apéndice 1).

Abbiatti, D. 693 (33), 4027 (19), 4057 (19), 4314 (21), 4330 (21), 4348 (21), 4462 (19); **Adler, M. J.** 30 (9); **Adler, V. T.** s.n. (9); **Aguilar, R. M.** 844 (32); **Aguilar, V.** 3 (19); **Aguirre, E.** 825 (32); **Ahumada, O.** 78 (32), 110 (19), 162 (30), 622 (4), 1134 (32), 1768 (30), 1803 (30), 1946 (30), 2148 (25), 3047 (30), 3095 (25), 4105 (30), 4264 (7), 4660 (7), 5212 (7), 6090 (23), 6430 (19), 7251 (23), 8294 (23), 8332 (23), 8445 (23), 8655 (6), 8958 (7), 8965 (7); **Ahun, E.** 29 (18); **Alaín, R.** 48 (33); **Alayòn, P.** 4 (2); **Alboff, N.** 190 (14), 3840 (19), s.n. LP 8498 (10), s.n. LP 8345 (8); **Alonso, J. M.** 370 (29), 572 (29); **Ambrosetti, J. A.** 1992 (33), 30877 (28a), 30994 (9); **Ameghino, C.** s.n. LP10004 (5a), s.n. LP10005 (5a), s.n. LP10006 (5a); **Ammann, E.** 111 (9), 112 (9), 113 (9); **Ancibor, E.** 4 (16), s.n. BAB 90126 (9), s.n. BAB 90186 (9); **Anderson, D. L.** 1518 (33), 1609 (18), 1631 (33), 1810 (18), 1815 (18), 1912 (21), 1915 (33), 2538 (33), 3076 (33), 3924 (33); **Antuña, C.** 68 (29); **Apochian, C.** 107 (16), 229 (16), 269 (16); **Aramayo, D.** 14 (19); **Arbo, M. M.** 909 (19), 1113 (10), 1246 (30), 1280 (25), 1283 (30), 1520 (19), 1903 (19), 1903 (17), 1916 (4), 1974 (30), 2429 (21), 5895 (30), 6873 (11), 7048 (30), 8888 (32), 9017 (23); **Archer, W. A.** 4233 (4); **Arenas, P.** 206 (4), 214 (4), 412 (19), 802 (16), 1878 (16), 2345 (32), 2378 (32), n-802 (16), s.n. CEFAPRIN 278 (33); **Argañarás, J. L.** 55 (2), 90 (19); **Arroyo, S. C.** 30 (5a), 343 (5a), 377 (13), 434 (5a), 481 (13); **Asp, O.** 108 (4), 157 (5a); **Atkinson, G.** s.n. SI 16063 (14); **August, L.** 100 (18); **Augusto, I.** s.n. PACA 34488 (4); **Azkue, D. de** s.n. BAB 91211 (21); **Bacigalupo, N. M.** 140 (2), 591 (29), 599 (32), 626 (21), 683 (32), 25747 (21), s.n. BAA 11645 (18); **Baer, G. A.** 6 (2); **Baez, J. R.** 173 (33); **Bailetti, E.** 58 (19); **Balegno, B.** 499 (32); **Barboza, G.** 422 (10); **Barkley, F. A.** 20Mz072 (3), 20Mz500 (9); **Barsini, O.** 731 (7); **Bartlett, H.**

H. 19410 (3), 19487 (5b), 19521 (9), 19862 (2), 20079 (33), 20416 (2); **Bartoli** 106/02–2 (13), 60/02–2 (13), 98/02–2 (3); **Basualdo, I.** 2891 (4); **Batista, L. R.** s.n. ICN 26838 (29); **Bazzi, G. R.** 230 (4); **Beck, G.** 191 (16), 6659 (6), 7470 (4), 9773 (19), 22163 (19); **Behn, F.** 8031 (3); **Belgrano, M. J.** 260 (19), 261 (30), 273 (29), 306 (4); **Bell, M.** 3 (16); **Beltrao, R.** s.n. SMDB 774 (19); **Beorchia, A.** 74 (16); **Bernard, L.** 499 (29); **Bernardello, L. M.** 706 (19), 803 (29), 811 (19); **Bianco-Cantero** 1209 (33); **Biganzoli, F.** 35 (4), 91 (19), 118 (10), 153 (4), 163 (19), 344 (10), 821 (19), 1461 (19), 1463 (4), 1465 (10), 1661 (19), 1725 (4), 1729 (30); **Biloni, J. S.** 6169 (33), 6247 (2), 6451 (12); **Birabén, M.** 3 (33), 525 (5a), 526 (5a), 532 (5a), 977 (33), 5019 (4), s.n. CTES 180546 (7), s.n. LP 906920 (32), s.n. LP 906985 (32); **Bissio** 239 (19); **Biurrum, F.** 235 (2), 427 (2), 2546 (19), 2690 (32), 3609 (33), 3628 (21), 4504 (33), 5035 (33), 5189 (16), 5242 (21), 5369 (6), 5405 (33), 5486 (33), 5624 (16), 5665 (16), 5739 (16), 6202 (9), 6240 (33), 6242 (21), 6350 (21), 6557 (21), 7040 (33), 7215 (33); **Bocco, M. E.** 1183 (33); **Böcher, T. W.** 768 (9), 1311 (5b), 2070 (28a), 2138 (3), 2145 (28a), 2395 (22); **Bocio, M. E.** 824 (29); **Boelcke, O.** 915 (14), 1252 (32), 1253 (29), 1272 (29), 1320 (29), 4073 (22), 4860 (32), 4923 (8), 4968 (32), 5140 (8), 6342 (8), 9360 (8), 9924a, b, c (28a), 10139 (5b), 10774 (9), 11236 (5b), 11777 (18), 11837 (21), 13611 (3), 13620 (3), 13747 (3), 15466 (9), 15675 (3), 15730 (3), 15799 (5a), 15842 (9), 15856 (9), 15858 (9), 16003 (21), 16643 (32), s.n. (2); **Boffa, P.** 148 (14), 330 (8), 1059 (19), 1093 (19); **Bonhers, A.** s.n. SGO 42528 (28a); **Bonifacio, M.** 703 (5a); **Bonsim, O.** 3 (19); **Bonzani, N.** 95 (33); **Bordignom, S.** 900 (4), 703 HUI 779 (19); **Bordón, A. O.** s.n. CTES 408675 (17); **Botta, S. M.** 109 (21), 252 (19), 269 (29), 270 (19), 272 (19), 275 (32), 291 (33), 292 (32), 293 (19), 294 (29), 299 (33), 311 (7), 330 (7), 332 (MO, SI) (7), 334 (7), 335 (7), 336 (7), 338 (7), 339 (7), 340 (7), 341 (7), 342 (7), 343 (7), 344 (7), 345 (7), 346 (7), 347 (7), 350 (7), 352 (19), 357 (19), 358 (33), 370 (22), 371 (19), 402 (18), 405 (9), 411b (18), 412 (18), 413 (18), 417 (18), 418 (18), 455 (5a), 457 (5a), 459 (5a), 461 (5a), 519 (33), 535 (5a), 552 (5a), 554b (13), 556 (13), 563 (5a), 687 (33), s.n. SI 26671 (9); **Bottino, O. J.** 16 (19); **Bowes, N. D.** 46 (29); **Brescia** 5075 (30); **Bridarolli, A.** 1002 (33), 1177 (33), 2564 (20), 3042 (30), 3232 1/2 (7); **Brown** 284 (19), 1521 (7); **Buchtien, O.** 433 (16); **Buck, P.** s.n. PACA 11535 (20), s.n. PACA 11605 (20); **Buenanueva, J.** s.n. (33); **Burkart, A.** 698 (29), 1005 (25), 1375 (19), 1424 (30), 2699 (19), 2780 (21), 3082 (8), 3616 (29), 3765 (14), 4331 (14), 4715 (21), 4797 (21), 4799 (21), 5127 (14), 5377 (16), 7017 (14), 7019 (14), 7494 (33), 8235 (14), 8474 (32), 8490 (29), 8678 (29), 9791 (29), 9884 (15), 9932 (27), 10191 (8), 10413 (33), 10414 (21), 10722 (33), 10796 (22), 10928 (21), 11003 (21), 11446 (7), 11536 (23), 11547 (12), 11640 (16), 12087 (33), 12546 (33), 12684 (21), 12748 (29), 12764 (32), 13193 (19), 13196 (19), 13199 (2), 13201 (2), 13202 (7), 13206 (21), 13364 (29), 13462 (19), 13828 (33), 13969 (21), 14081 (10), 14250 (9), 14251 (9), 14252 (9), 14269 (13), 14272 (13), 14274 (5a), 14277 (5a), 14877 (28a), 14903 (3), 15134 (14), 15226 (30), 15838 (21), 17570 (4), 17859 (29), 17961 (19), 18149 (29), 18372 (32), 18389 (4), 18396 (25), 18445 (29), 18561 (4), 18839 (25), 18871 (4), 19015 (29), 19168 (21), 19221 (18), 19469 (29), 19550 (30), 19556 (19), 19658 (11), 19987 (24), 20114 (33), 20139 (7), 20789 (33), 20846 (22), 21369 (32), 21553 (24), 21887 (29), 21890 (19), 22072 (19), 22073 (22), 22091 (22), 22279 (29), 22280 (32), 22281 (19), 22284 (29), 22285 (29), 22286 (29), 22288 (32), 22289 (32), 22290 (32), 22292 (32), 22293 (29), 22380 (29), 22403 (14), 22699 (SI, SP) (19), 22703 (29), 22707 (32), 22708 (29), 23094 (29), 23455 (32), 23456 (32), 23457 (32), 23458 (32), 23460 (21), 23462 (32), 23466 (29), 23795 (32), 23797 (29), 23798 (21), 23801 (29), 23802 (32), 23803 (29), 23804 (29), 23806 (29), 23807 (32), 23808 (29), 23908 (29), 24014 (29), 24230 (29), 24231 (29), 24903 (29), 25165 (24), 25171 (24), 25177 (19), 25399 (29), 25402 (32), 25409 (29), 25428 (27), 25430 (29), 25431 (SI, SP) (32), 25432 (32), 25434 (29), 25638 (29), 25639 (29), 25640 (29), 25641 (21), 25642 (29), 26344 (29), 26353 (27), 26530 (19), 26547 (12), 26566 (19), 26597 (21), 26600 (2), 26606 (2), 26615 (29), 26616 (32), 26622 (32), 27052 (29), 27055 (14), 27057 (31), 27338 (29), 27350 (29), 27356 (29), 27358 (4), 27594 (32), 27756 (29), 27757 (32), 27758 (32), 27759 (29), 28061 (14), 28062 (29), 28065 (29), 28069 (21), 28071 (29), 28075 (29), 28077 (29), 28194 (19), 28194 (21), 28417 (29), 28420 (4), 28421 (10), 28815 (19), 28816 (29), 28817 (29), 28818 (29), 28820 (29), 28821 (29), 28822 (29), 28827 (32), 28830 (21), 28965 (29), 29014 (24), 29452 (25), 29459 (29), 29461 (29), 29462 (29), 29464 (29), 30019 (29), 30093 (29), 30094 (29), 30096 (29), 30102 (29), 30103 (14), 30106 (29), 30111 (27), 30114 (29), 30118 (29), 30119 (29), 30121 (29), 30570 (21), 30571 (21), 30581 (2), 30586 (19), 30587 (32), 30588 (32), 30591 (6), 30592 (2), 30594 (2), 30603 (7), 30609 (19), 30610 (7), 30611 (7), 30612 (7), 31055 (29), 31061 (29), 31065 (17), 31069 (30), 31070 (10), s.n. (29), s.n. SI 20461 (29), s.n. SI 27706 (29), s.n. SI 27708 (29); **Burmeister, C.** 25 (33); **Butzke, A.** 7758 (20), 7892 (10); **Cabezas, V.** s.n. SI 23191 (16); **Cabral, E.** 270 (19); **Cabrera, A. L.** 48 (5a), 509 (14), 1021 (33), 1099 (33), 1241 (14), 1584 (14), 1618 (14), 1962 (10), 2431 (14), 3226 (8), 3388 (19), 3401 (14), 3852 (21), 4891 (14), 5179 (29), 5278 (21), 5378 (14), 5473 (21), 6570 (21), 6671 (18), 7181 (32), 7195 (29), 7312 (19), 7772 (16), 7968 (19), 8058 (29), 8459 (29), 8866 (16), 8981 (16), 9174 (16), 9610 (14), 9850 (29), 10228 (29), 10250 (19), 10352 (8), 10828 (32), 11142 (3), 11606 (19), 11957 (11), 12105 (16), 12763 (19), 13940 (16), 14514 (23), 14780 (29), 14835 (18), 14894 (18), 15228 (16), 15388 (16), 15474 (16), 15759 (7), 15763 (7), 15813 (7), 15830 (23), 15994 (23), 16031 (7), 16074 (23), 16083 (23), 16317 (33), 16414 (33), 16671 (33), 16705 (33), 16747 (33), 16967 (12), 17128 (8), 17276 (21), 17331 (19), 17625 (16), 17660 (16), 17719 (16), 17729 (16), 18082 (33), 18338 (12), 18658 (9), 18687 (3), 18693 (3), 18767 (18), 18952 (16), 19012 (16), 19128 (9), 19390 (18), 19402 (21), 19413 (18), 19433 (18), 19458 (21), 19547 (9), 19583 (18), 20142 (12), 20393 (33), 20780 (7), 20799 (23), 20852 (27), 20908 (21), 21053 (21), 21054 (33), 21205 (9), 21903 (9), 21904 (9), 21970 (9), 22009 (2), 22057 (21), 22205 (21), 22279 (7), 22568 (21), 23866 (7), 24026 (7), 24458 (16), 24508 (16), 24631 (33), 24782 (19), 25417 (33), 25418 (32), 25437 (33), 26473 (7), 27008 (33), 27041 (16), 27141 (33), 27147 (33), 27208 (22), 27257 (33), 27451 (16), 27469 (4), 27551 (6), 27626 (29), 27656 (29), 27751 (32), 27927 (7), 27974 (12), 28044 (23), 28090 (24), 28173 (29), 28190 (11), 28364 (27), 28488 (10), 28499 (11), 28530 (17), 28555 (17), 28560 (4), 28610 (4), 28627 (19), 28643 (30), 28737 (10), 28744 (10), 28767 (11), 29016 (32), 29030 (29), 29044 (30), 29180 (4), 29254 (29), 29258 (17), 29333 (17), 29363 (4), 29513 (18), 29520 (29), 29531 (33), 29549 (33), 29622 (33), 29633 (33), 29634 (19), 29638 (21), 29665 (21), 29672 (33), 29673 (21), 29696 (22), 29735 (2), 29903 (23), 29909 (23), 29965 (2), 29973 (19), 30369 (23), 30403 (7), 30497 (19), 30574 (16), 30726 (16), 30726 (2), 30753 (33), 30795 (22), 30849 (22), 30937 (12), 30942 (23), 31066 (33), 31169 (16), 31305 (33), 31321 (7), 31433 (7), 31554 (7), 31659 (16), 31889 (2), 32070 (7), 32079 (7), 32102 (23), 32208 (23), 32214 (7), 32270 (23), 32315 (29), 32452 (16), 32813 (18), 32897 (3), 32992 (9), 33015 (13), 33051 (13), 33202 (5a), 33272 (5a), 33465 (9), 33566 (6), 33602 (6), 33637 (32), 33908 (7),

33944 (7), 33947 (23), 33979 (7), 34040 (23), 34058 (23), 34062 (7), 34120 (23), 34139 (5a), 34384 (23), 34456 (23), 34464 (6), 34561 (21), 34588 (19), 34634 (7), 34642 (23); **Cáceres, S.** 17 (27), 113 (19), 187 (32); **Cajal, J. L.** 68 (16); **Calderón, C. E.** 1084 (33), 1400 (21); **Camargo, O. R.** 33 (19), 502 (19); **Cano, E.** 490 (32), 491 (30), 491 1/2 (29), 513 (29), 800 (9), 1875 (29), 1901 (32), 1962 (29), 2509 (33), 2559 (9), 2590 (18), 2629 (2), 2686 (18), 2688 (18), 2715 (18), 2762 (33), 2765 (33), 3024 (29), 3031 (9), 3288 (29), 3394 (18); **Cano, J. A.** 1688 (19), 1756 (33), 1885 (19), 1917 (19), 2240 (33), 2367 (18), 2413 (33), 2788 (32), 2929 (29), 2937 (33), 4715 (29); **Capell, P. J.** s.n. (19); **Cárdenas, M.** 105 (16); **Carette, E.** 35 (15), 39 (28a), 157 (15), 270 (15), 333 (9), 339 (5b), 344 (28a), 345 (28a), 346 (28a), 385 (28a), 493 (29), 496 (29), 504 (19), 2558 (9), 2565 (28a), s.n. SI 3381 (5b), s.n. SI 3432 (28a); **Carnevalli, R.** 8 (29), 2286 (30), 2621 (10), 4260 (10), 4363 (19), 4408 (25), 4967 (26), 5010 (26), 5794 (25); **Casarim, E.** s.n. HUI 4145 (19); **Castañeda Vega** 60 (32), 61 (2); **Castellanos, A.** 121 (33), 166 (29), 441 (19), 522 (21), 713 (21), 1431 (2), 20158 (9), 20189 (5b), 20586 (9), 27/890 (16), s.n. BA 23637 (16), s.n. BA 30/1753 (17), s.n. BA 6182 (5a), s.n. LIL 36667 (33), s.n. SI 3568 (21); **Cervi, A. C.** 2715 (4), 3396 (4); **Chalukian, S.** 5 (12), 533 (7); **Champing, A.** 20347 (4), AC 20436 (23), AC 20581 (6), AC 22891 (7); **Chiarelli, C.** s.n. BAB 91546 (19); **Chicchi, A.** 36 (9); **Cialdella, A. M.** 293 (16), 307 (16), 356 (21), 442 (16), 496 (16), 572 (7); **Claren, F.** 11468 (16); **Clem** s.n. PACA 95227 (19); **Clos, E.** 6007 (10); **Clough, J.** de s.n. (33); **Cocucci, A. A.** 2244 (5a), 2358 (3), 2632 (12), 3023 (29), 3066 (29), 3093 (19), 3146 (10); **Coe Teixeira, B.** 48 (19); **Coelho, G. C.** 364 (19); **Contreras, J.** s.n. (29); **Cordeiro, J.** 1615 (10); **Cordini, J. R.** 17 (2), 32 (19); **Cordo, H.** 126 (32), s.n. (4), s.n. (7), s.n. (19), s.n. (19), s.n. (19), s.n. (19), s.n. (22), s.n. (22), s.n. (2), s.n. (2), s.n. (33), s.n. (33), s.n. (33); **Coro, M.** 94 (23), 537/78 (16), 603/78 (23), A.399 (23); **Correa, A.** 188 (19); **Correa, M. N.** 2456 (18), 3180 (9), 3656 (13), 3683 (3), 3693 (13), 3713 (9), 3873 (13), 3964 (5a), 4284 (12), 4498 (19), 4967 (18), 4969 (18), 4988 (18), 5227 (29), 5268 (29), 6257 (13), 6418 (5a), 6810 (9), 7508 (23), 7582 (32), 7648 (32), 7688 (2), 7833 (3), 7904 (5a), 8036 (3), 8786 (29), 9523 (18), 9594 (9), 9726 (18), 9738 (18), 9974 (3), 10131 (18), 10133 (18), 10134 (18), 10137 (9), 10230 (5a), 10291 (5a), 10359 (5a), 10382 (13), 10469 (3), 10480 (3), 10483 (3), 10510 (3), 18058 (29), 18062 (32), 9574–9594? (9), s.n. BAA 2346 (29), s.n. BAA 2357 (29), s.n. BAA 2357 (29), s.n. BAA 2388 (21), s.n. BAA 2428 (29), s.n. BAA 2429 (SI) (21), s.n. SI 18071 (19); **Coste, A.** 1020 (21); **Covas, G.** 296 (18), 542 (33), 619 (28a), 626 (3), 929 (3), 1033 (33), 1034 (33), 1068 (33), 1094 (21), 1197 (33), 2960 (9), 15105 (16), s.n. (15), s.n. (16), s.n. (18), s.n. (33), s.n. (33); **Crespo, S.** 1784 (18), 1810 (18), 2503 (9), 2561 (18), s.n. SI 26458 (24); **Cristóbal, C. L.** 1141 (19), 1210 (32), 1241 (32), 1619 (29); **Cuadrado, G.** 16 (19), 17 (4); **Cuezzo, A. R.** 716 (33), 767 (7), 2054 (33), 2091 (33); **da Costa Sacco, J.** 646 (29); **Daciuk, J.** 13 (9), XXXIII-10 (9), XXXIII-11 (9), XXXIII-14 (18); **Daguirre** s.n. BA 28/993 (17); **D'Antoni** 148 (33); **Daviña, J.** 511 (20); **Dawson, G.** 13 (29), 35 (33), 158 (33), 524 (33), 1173 (3), 1595 (28a), 1758 (2), 1768 (19), 2093 (3), 3045 (19), 3067 (21), 3165 (33), 3416 (33), 3491 (33), 3504 (32); **De Azkue, D.** s.n. BAB 91208 (21), s.n. BAB 91319 (21); **De Egea, J.** 139 (4); **de la Sota, A.** 5 (32), 51 (32), 217 (33), 275 (33), 411 (33), 436 (33), 673 (33), 1563 (33), 1624 (33), 1731 (33), 1959 (33), 2147 (33), 2166 (33), 2308 (33), 3033 (33), 3068 (33), 3163 (33), 3787 (33), 3833 (33), 4066 (33), 4156 (33), 4309 (33); **De Loach, C. J.** 153 (4); **De Marco de Kreibon, E.** 117 (5a); **Degen, R.** 343 (19); **Deginani, N. B.** 490 (16), 611 (29), 980 (19), 1367 (19), 1837 (29), 1868 (19); **Del Castillo** 30 (19); **Del Puerto** 1421 (24), 1626 (32), 5746 (14), 11325 (29), 11331 (21), 11486 (29), 11586 (29), 11637 (9); **Dell'Arciprete, A. C.** s.n. BACP 2213 (16); **Delucchi, G.** 243 (33), 2511 (9); **Dematteis, M.** 704 (25), 749 (19); **Denalpfi, R. F.** 28 (2); **Denham, S.** 53 (30); **Descole** 1548 (19); **Dheroten, A.** s.n. SI 3371 (29); **Díaz, M. O.** s.n. (4), s.n. (32), s.n. (32); **Díaz, W.** s.n. SGO 42525 (15), s.n. SGO 54795 (15); **Diem, J.** 947 (3), 1497 (20), 1560 (19), 1568 (4), 3203 (13); **Diers, L.** 20 (2), 66 (22), 69 (19), 103 (21); **Digiacomo, A.** 49 (32), 51 (25); **Digilio, A.** 2028 (33); **Dilullo** 22 (2); **Dominguez** s.n. (16); **Donat, A.** 77 (32), 219 (5a); **Duarte, A. P.** 6309 (14); **Duré, R.** 169 (10); **Dusén** 6308 (29); **Emmerich, M.** s.n. HB 21271 (27); **Emrich, K.** s.n. PACA 30011 (20), s.n. PACA 32279 (20), s.n. PACA 35908 (20), s.n. PACA 50183 (20), s.n. PACA 51274 (19); **Escobar** 55 (19); **Escoiaro** 38 (18); **Eskuche, U.** 189 (9), 240 (3), 549 (4), 940 (3), 1477-14 (9), 2936–53 (19), 3087-26 (19); **Eyerdam, W. J.** 22355 (19), 22598 (23), 23039 (8); **Ezcurra, C.** 6 (29), 517 (18), 519 (33), 562 (33); **Fabris, H. A.** 9 (19), 344 (29), 569 (9), 660 (29), 786 (29), 842 (9), 868 (5b), 1033 (33), 1493 (19), 1625 (33), 1752 (16), 1800 (16), 1810 (16), 2506 (19), 2686 (18), 2728 (33), 2973 (7), 2986 (7), 3191 (10), 3538 (23), 3601 (16), 3646 (16), 4447 (23), 4461 (23), 4874 (21), 5022 (18), 5031 (23), 5034 (7), 5072 (23), 5288 (23), 5331 (23), 5425 (12), 5762 (12), 5923 (12), 5933 (12), 6593 (32), 6636 (LP, CTES) (8), 7116 (10), 7207 (4), 7270 (23), 7284 (23), 7333 (23), 7350 (20), 7356 (14), 7435 (20), 7672 (23), 7719 (16), 7720 (16), 7771 (16), 7792 (16), 7953 (20), 8136 (19), 8242 (7), 8372 (16), 8395 (16); **Falcone** 5541 (22), 5951 (19); **Felippone, F.** 2007 (24), 2010 (24), 2012 (24), 2053 (19), 2129 (24), 2130 (19), 2240 (24), 2324 (24), 2353 (19), 2561 (24), 2724 (19), 2725 (24), 2728 (19), 2742 (24), 2747 (24), 2767 (19), 2784 (24), 2791 (24), 2847 (8), 2874 (24), 2937 (24), 3040 (19), 3068 (24), 3071 (24), 3087 (24), 3147 (29), 3159 (19), 3249 (24), 3271 (19), 3364 (19), 3382 (24), 3386 (24), 3516 (24), 3995 (19), 4659 (24), 5915 (24), 5972 (24), 5977 (24), 6028 (24), 6118 (8), 6136 (19), 6146 (24), 6975 (8), 398a (24), 2605 bis (24), 5924b (19); **Fernández, A.** 215 (29); **Fernández, J. G.** 1068 (25); **Ferraro, L.** 1956 (21), 4128 (33); **Ferreira, A.** 680 (19), s.n. ICN 7385 (20), s.n. ICN 7414 (20); **Ferrucci, S.** 578 (19); **Fiebrig, K.** 6452 (10); **Fiedler, R.** 68 (5a), 69 (3); **Filho, A. A.** s.n. SMDB 1179 (19); **Filipov, A.** 52 (32), 53 (4); **Fischer, W.** 59 (9); **Fortunato, R. H.** 1272 (17), 1274 (2), 2194 (4), 2223 (32), 2295 (32), 2365 (4), 2408 (25), 5532 (16), 6430 (19), 6818 (19), 8014 (10); **Forzza, R. C.** 1941 (11); **Fossati, J. L.** 957 (29); **Franceschi** 367 (29); **Franco, E. T. H.** s.n. ICN 64366 (20); **Frenguelli, J.** 18 (32), 137 (2), s.n. (33), s.n. (9), s.n. LP894645 (9); **Frick, Y.** 57 (9); **Friderichs** s.n. PACA 26767 (19); **Galetto, L.** 22 (32), 29 (19), 56 (33), 64 (19), 65 (33), 74 (33), 75 (19), 94 (19), 96 (33), 144 (21), 153 (19), 162 (22), 222 (23); **Gallardo, A.** 59 (5a), 60 (5a); **Gallardo, C.** s.n. (10); **Galli** 26 (19); **Gallinal, J. P.** 135 (24), 492 (27), 1375 (24), 1433 (24), 1821 (24), 1958 (24), 5262 (27), B-810 PACA 27997 (21); **Gamerro, J. C.** 58 (4), 165 (20), 1022 (14); **Garaventa, A.** 5759 (3), 5835 (3); **Garolera-Romero** 44 (12), 56 (32); **Gerling, G.** 135 (5b), 728 (5a), 913 (5a); **Gez, J. W.** 127 (33), 133 (33); **Giardelli, M. L.** 18 (33), 151 (33), 168 (19), 223 (29), 413 (33), 443 (29), 622 (29), 627 (29), 693 (33), 809 (21), 1034 (29), 1052 (33), 14923 (29), s.n. SI 3573 (19); **Gilbert, F.** s.n. CTES 408677 (17); **Giménez, A. M. de** 141 (29), 383 (29), 392 (19); **Giraldi-Deiro, A. M.** 1801 CNPO 3376 (21), s.n. CNPO 715 (19), s.n. CNPO 1111 (19), s.n. CNPO 1210 (21); **Goldenberg, R.** 640 (4); **Gomes, T.** s.n. SMDB 9750 (19); **Gómez, M.** 5896 (28a), s.n. SI 3353 (32), s.n. SI 3368 (29), s.n. SI 3368 (29); **Gómez, R.** s.n. BAB 11990 (19); **Gómez Sosa, E.** 238 (22); **Gonzáles Arzoc, E.**

912 (3); **Gonzáles, F.** 444 (19); **Grassi, D.** 2227 (33); **Grazziotin, G.** 2135 (23); **Grondona, E.** 58 (29), 5806 (5a), 5807 (5a), 7057 (19); **Guaglianone, E. R.** 183 (29), 196 (32), 210 (21), 221 (30), 222 (30), 223 (10), 224 (29), 225 (29), 230 (29), 252 (32), 286 (17), 295 (4), 301 (4), 421 (25), 436 (4), 526 (29), 581 (32), 807 (30), 889 (19), 903 (11), 904 (26), 1314 (29), 1459 (33), 1844 (21), 2184 (32), 2186 (4), 2216 (4), 2378 (33), 2508 (30), 2508 (30), 2629 (7), 2643 (23), 3236 (3), 3283 (19); **Guerrero, A.** 27 (5a), 40 (5a); **Guglialmelli, L.** s.n. SI 27712 (29), s.n. SI 27712 (29); **Guiñazú, G. R.** 112 (33), p.p. 226 (9), p.p. 226 (27); **Guitman, M. R.** s.n. LP 929176 (21), s.n. LP 929179 (19); **H. A. L.** 5365 (16), 6527 (28a), 7211 (18), 7255 (18); **Haene, E. H.** 201 (18), 561 (18), 789 (33), 1078 (3), 1758 (16), 1989 (16), 2014 (16), 2089 (16); **Hagelund, K.** 8139 (11), 9564 (10), 11680 (24), 13274 (10), 14128 (17); **Harley, R. M.** 28001 (19), 28011 (32), 28014 (4), 28039 (11); **Hartwing, W.** s.n. CONC 11552 (28a); **Hassler, E.** 192 (32), 1396 (19), 1466 (10), 1603 (4), 1680 (25), 11052 (11), 11312 (14), 12335 (32), 12411 (4); **Hatschbach, G.** 1993 (19), 3067 (20), 3138 (20), 4218 (4), 4369 (10), 7444 (4), 9946 (4), 14967 (20), 15008 (20), 15041 (20), 15051 (4), 15522 (20), 18321 (20), 18368 (4), 19774 (4), 22637 (20), 23670 (20), 23852 (4), 23884 (4), 25241 (4), 25738 (20), 26081 (20), 27219 (19), 30760 (4), 30817 (4), 34547 (4), 35172 (10), 46164 (20), 47610 (29), 49225 (4), 49380 (19), 50552 (19), 52326 (11), 52352 (19), 57866 (19), 58800 (4), 71822 (19), 72415 (4), 72697 (19); **Heidler** s.n. PACA 11252 (19); **Henz** s.n. PACA 25970 (19), s.n. PACA 29591 (29), s.n. PACA 32539 (19), s.n. PACA 33438 (19); **Herb. Inst. Fitotécnico** 9 (23); **Hernonem, S.** s.n. (29); **Herrera, S. M. E.** 158 (1), 370 (33); **Herter, W. G.** 19 (19), 85 (32), 1805 (8), 181a (24), 181b (24), 181c (24), 750A (21), 750B (21); **Hicken, C. M.** 21 (21), 33 (9), 54 (9), 74 (8), 78 (21), 228 (32), 307 (19), 308 (4), 473 (19), 474 (29), 478 (29), 491 (29), 571 (29), 891 (29), s.n. (8), s.n. (21), s.n. SI 1407 (29), s.n. SI 27704 (29), s.n. SI 27705 (29), s.n. SI 27709 (29), s.n. SI 27711 (29), s.n. SI 3345 (19), s.n. SI 3347 (32), s.n. SI 3349 (19), s.n. SI 3354 (19), s.n. SI 3355 (19), s.n. SI 3366 (19), s.n. SI 3367 (29), s.n. SI 3369 (29), s.n. SI 3370 (29), s.n. SI 3372 (29), s.n. SI 3373 (29), s.n. SI 3374 (29), s.n. SI 3375 (29), s.n. SI 3378 (29), s.n. SI 3380 (9), s.n. SI 3434 (29), s.n. SI 3435 (29), s.n. SI 3440 (21), s.n. SI 3442 (21), s.n. SI 3443 (21), s.n. SI 3449 (32), s.n. SI 3450 (32), s.n. SI 3571 (2); **Hieronymus, G.** s.n. (33), s.n. (33); **Hjerting, J. P.** 31 (23), 9471 (22); **Holmberg, E. L.** s.n. SI 10467 (7), s.n. SI 10449 (19); **Huajardo, E. D.** de 432 (18), 1715 (15), 2548 (15), 3013 (15), 3028 (9), 3114 (9), 3212 (28a), 3738 (15), 3761 (9), 4397 (9), 4734 (33); **Huidobro, A. M. R.** 3493 (32), 3565 (32), 3603 (32); **Humbert, H.** 21218 (7); **Hunziker, A. T.** 1212 (7), 2302 (19), 2568 (22), 3040 (16), 4584 (18), 5094 (33), 5107 (19), 5160 (22), 9353 (29), 16107 (29), 16418 (29), 17940 (2), s.n. (2); **Hunziker, J. H.** 384 (18), 2148 (16), 2160 (19), 2334 (29), 3128 (13), 6463 (21), 6464 (33), 6467 (2), 7817 (16), 8110 (16), 8132 (16), 8312 (9), 8330 (8), 9785 (2), 9897 (33), 9898 (33), 9937 (29), 9947 (20), 9950 (4), 9951 (4), 9952 (4), 9956 (30), 9963 (4), 9966 (30), 9975 (25), 9978 (32), 9979 (29), 10475 (16), 10660 (7), 10749 (29), 11300 (13), 11504 (21), 11510 (29), 11525 (21), 11562 (21), 11829 (10), 12022 (21), 12023 (21), 12061 (21), 12072 (21), 12742 (12), 12754 (19), 12778 (12), 13071 (7), s.n. (32); **Hurrell, J.** 4902 (32), 4913 (32), 5207 (32), 5217 (29), 5789 (29); **Ibarrola, T.** 341 (30); **Illín, N.** 1123 (5a), s.n. LP10001 (5a); **Insaurralde, I.** 1139 (10); **Irgang, B.** s.n. ICN 51770 (29), s.n. ICN 81222 (20); **Iudica** 49 (23), 120 (16), 186 (12); **Izaguirre** 9584 (8), 11887 (29); **J. R.** 60 LP10002 (5a); **Jiles, C.** 730 (28a), 3459 (28a); **Jiménez, B.** 1362 (14); **Job, M. M.** 1410 (19), 1414 (8), 1898 (33), 1901 (33), 1902 (33), 2949 (19), 2973 (9), s.n. LP 903550 (19), s.n. LP 905475 (32), s.n. LP 909080 (32), s.n. LP 909216 (32); **Jörgensen, P.** 86 (12), 1026 (33), 1028 (32), 1297 (21), 1298 (23), 2465 (29), 2466 (32), 2469 (17), 2470 (4), 2477 (25), 2636 (30), 3769 (10), 3771 (4), 3772 (32), 3773 (25), 3774 (25), 86a (12); **Jozami, J. M.** 143 (32); **Jurado, D.** s.n. SI 27707 (29); **Kaufmann** 4954 (21); **Kegler, A.** 14972 (20); **Keller, H.** 417 (19), 418 (30), 2830 (20); **Kermes, E.** 3 (27); **Kiesling, R.** 1044 (33), 1065 (19), 1066 (33), 1127 (19), 1202 (33), 1224 (12), 1236 (23), 1242 (2), 1295 (16), 1360 (28a), 1564 (16), 1925 (19), 1926 (21), 2939 (33), 3034 (18), 3095 (33), 3115 (33), 3127 (3), 3281 (16), 3323 (33), 3327 (33), 3347 (33), 3538 (16), 3573 (2), 3674 (16), 3724 (19), 3877 (16), 3968 (7), 4032 (33), 4139 (3), 4214 (3), 4239 (33), 4398 (33), 4439 (3), 4459 (3), 4464 (33), 4536 (16), 4546 (16), 4577 (16), 4645 (16), 4655 (13), 4708 (33), 4780 (3), 4788 (3), 4798 (33), 4847 (33), 4874 (9), 4966 (33), 4993 (21), 5004 (33), 5071 (19), 5112 (19), 5204 (16), 5357 (21), 5426 (7), 5460 (33), 5480 (7), 5481 (33), 5482 (7), 5567 (7), 5568 (7), 5569 (7), 5571 (7), 5575 (7), 5576 (7), 5578 (7), 5579 (7), 5581 (7), 5582 (7), 5583 (7), 5584 (7), 5591 (7), 5592 (7), 5593 (7), 5594 (23), 5641 (23), 5767 (12), 5768 (12), 5860 (22), 5907 (2), 5916 (33), 6064 (33), 6254 (16), 6284 (3), 6314 (28a), 6317 (33), 6324 (33), 6496 (16), 6948 (28a), 6963 (28a), 6978 (13), 7068 (16), 7700 (16), 7861 (33), 7916 (16), 7941 (16), 8045 (16), 8071 (19), 8108 (18), 8187 (7), 8282 (21), 8316 (7), 8562 (28a), 8582 (16), 8764 (16), 8839 (28a), 9082 (16), 9166 (13), 9682 (4), 10069 (13), 10154 (13), 10226 (9), s.n. (16); **Killeen, T.** 4261 (6); **King, D. O.** 246 (19); **Klein, R. M.** 4293 (20), 4406 (20), 4881 (20), 5084 (20), 5084a (20); **Knob, A.** 5674 (4), 6142 (14); **Koslowsky, J.** 12352 (5a); **Krapovickas, A.** 673 (32), 1592 (23), 1624 (7), 1741 (2), 1824 (9), 1908 (33), 2324 (4), 2427 (19), 2752 (29), 2924 (21), 3086 (8), 3317 (14), 5408 (28a), 6403 (29), 6408 (19), 6428 (21), 7433 (22), 11442 (32), 11668 (19), 12134 (4), 12550 (10), 13080 (4), 13085 (30), 13087 (32), 13184 (25), 13641 (30), 14581 (13), 14872 (4), 14985 (30), 15163 (19), 15492 (30), 15588 (29), 15838 (32), 15910 (4), 16015 (4), 16298 (24), 16357 (25), 16373 (30), 16725 (30), 16791 (26), 16794 (30), 17226 (10), 17315 (4), 17388 (2), 17516 (21), 17805 (29), 17824 (29), 17972 (10), 18053 (4), 18520 (32), 18939 (19), 19272 (6), 19436 (32), 19495 (6), 19561 (32), 19932 (29), 20129 (4), 20536 (22), 21073 (30), 21181 (26), 21300 (11), 21440 (19), 21608 (11), 21609 (26), 22284 (29), 22288 (19), 22360 (21), 22425 (9), 22730 (4), 22778 (29), 22995 (20), 23981 (30), 24227 (10), 24385 (31), 24989 (11), 25274 (25), 25731 (19), 25759 (32), 26004 (11), 26039 (32), 26114 (19), 26138 (30), 26138 (17), 26141 (26), 26143 (4), 26689 (7), 26701 (7), 27068 (32), 28715 (4), 28956 (11), 29027 (10), 30520 (2), 31011 (6), 33701 (11), 36784 (20), 36832 (11), 37538 (30), 38526 (19), 38648 (7), 39050 (6), 39276 (23), 41233 (11), 44340 (4), 47471 (33), 47561 (21), 20129a (29); **Kristensen** 313 (7); **Kuhlmann, M.** 3717 (31); **Kuntze** s.n. LP 8418 (33); **Kurtz, F.** 5605 (5a), 9691 (28a); **Lagiglia, H. A.** 953 (9), 1089 (18); **Laite** s.n. (20); **Landrum, L. R.** 8627 (32); **Lanfranchi, A. E.** 496 (14), 628 (33), 753 (14), 818 (33), 1070 (33), 1079 (29), 1550 (21), 1567 (33), 1638 (29), 1717 (19), 1737 (29), 1852 (29); **Lavia, G.** 2 (32); **Lee Anderson, D.** 1813 (33); **Legname, P. R.** 4036 (23), 4432 (12), 4075c (7), 5027c (23); **León, R.** 2509 (5a); **Levi, U.** 3214 (28a); **Lichtenstein, J. S. de** s.n. (19), s.n. SI 17476 (32), s.n. SI 17479 (29), s.n. SI 18104 (19), s.n. SI 27710 (29), s.n. SI 27713 (29), s.n. (24), s.n. SI 18102 (33); **Lima, D.** s.n. ICN 20957 (29); **Linch** s.n. (29); **Lindeman, J. C.** 2788 (4), 3717 (4), 3772 (19); **Lizer** s.n. SI 3376 (29); **Llamas, A.** de 142 (14), s.n. BAB 1542 (10); **Looser, W.** 72 (33), 117 (21); **López, A. G.** 1 (14);

López, N. 22 (16); **Lourteig, A.** 487 (19), 515 (19), 2030 (19); **Lurvey, E.** 3 (19), 215 (30); **Luteyn, J. L.** 6515 (16); **Luti, R.** 501 (13), 4104 (2), 4493 (33), 5879 (28a); **Lynelo** s.n. (29); **M. M?** 14 (3); **Mahus, J.** s.n. PACA 86473 (29); **Maldonado, R. B.** 90 (33), 419 (2), 472 (32), 833 (6), 968 (33), 1018 (33), 1436 (33), s.n. (9), s.n. LP 48417 (9); **Mallo, M.** s.n. BAB 18521 (3); **Malvárez, M. R.** 609 (7), 1365 (32); **Marazzi, B.** BM 265 (4); **Marchesi** 10045 (27); **Marchett, F.** 404 (19); **Marchionni, J. M.** 8 (4); **Marchioretto, M. S.** 58 PACA 87049 (19); **Marin, G.** 249 (10); **Marin, O.** 11 (23); **Marq** 56 (21); **Marquez** 36 (18); **Marquez, S.** 43 (5b), 102 (9); **Martinez Achembachi, G.** 899 (33), 1000 (4); **Martínez Crovetto, R.** 443 (8), 2738 (29), 2739 (29), 3378 (7), 4937 (29), 5527 (29), 5965 (30), 6088 (7), 6107 (29), 6151 (9), 6350 (19), 7250 (16), 8160 (4), 8400 (4), 8862 (4), 8976 (4), 9444 (4), 9498 (4), 10174 (4), 10390 (29), 10392 (29), 11114 (19), 11227 (4), 11392 (17), g 361 (10); **Martínez, A.** s.n. BAA 9409 (4), s.n. BAA 9459 (32), s.n. BAA 9553 (29), s.n. BAA 9578 (32), s.n. BAA 9693 (17); **Martínez, L.** 12490 (19); **Martínez, W. J.** 2 (32); **Maruñak, V.** 124 (32), 126 (4), 134 (10), 294 (19); **Mauri, E.** 84 (8); **Mazzoti** s.n. Herb. Inst. Sta. Catalina 641 (2); **Medán, D.** 670 (21); **Medinaceli, M.** 3 (16), s.n. (6), s.n. (16); **Medrano, G.** 7631 (18); **Meglioli, C.** 160 (16); **Meglioli, S.** 27 (33), 60 (33); **Merck, H.** s.n. SI 3576 (14); **Mereles, F.** 1428 (4), 1980 (4), 8171 (10); **Meyer, T.** 139 (29), 143 (32), 926 (23), 2158 (31), 2409 (29), 2673 (32), 8685 (7), 10154 (32), 13073 (33), 13243 (33), 13425 (33), 13753 (33), 18051 (16), 34401 (16), 141a (29), 142 (29), 680 (17); **Michel, R.** 95 (19), 443 (6); **Millán, A. R.** 300 (29), 617 (33), 665 (21), 778 (33), 779 (19); **Molfino** s.n. (20); **Mongieri** 45 (10); **Montero O. G.** 12282 (28a); **Montes, J. E.** 1747 (10), 1825 (4), 2278 (4), 2279 (19), 2454 (19), 2521 (10), 3988 (4), 3989 (19), 10913 (30), 11207 (26), 12429 (17), 12445 (30), 12502 (4), 12539 (30), 12570 (10), 12609 (10), 12851 (11), 12961 (11), 12989 (10), 15434 (17), 15449 (26), 15464 (32), 15477 (4); **Monticcelli, J.** C74 (21), I-6 (9), J-8 (29); **Montiel, J. C.** s.n. SI 27714 (29); **Moreira Filho, H.** 353 (19); **Morel, I.** 38 (17), 199 (32), 419 (17), 789 (32), 1008 (32), 1178 (17), 1493 (17), 2003 (32); **Morello, J.** 4046 (29), 5289 (33), 16931 (19); **Morrone, O.** 120 (32), 599 (4), 1119 (30), 1134 (19), 1663 (4), 1868 (4), 2673 (16), 3032 (12), 3154 (6), 3429 (23), 3814 (23), 4469 (7), 4492 (12), 4612 (23), 4642 (7), 5209 (29), 5224 (29), 5232 (19), 5255 (27), 5302 (29), 5323 (19), 5354 (29), 5413 (21), 5471 (21), 5492 (29), 5749 (3), 5783 (29); **Moyano** s.n. LP 10003 (5a); **Mroginski, L. A.** 2 (19), 464 (19), 501 (32); **Múlgura, M. E.** 158 (16), 210 (16), 240 (33), 741 (33), 773 (21), 802 (33), 1123 (29), 1129 (19), 1135 (18), 1291 (16), 1417 (23), 1564 (30), 1693 (10), 1722 (4), 2027 (30), 2057 (4), 2119 (19), 2347 (19), 2849 (4), 2911 (4), 2928 (33), 3489 (29), 3490 (19), 3746 (4), 3758 (19), 3777 (4), 3786 (30), 3795 (19), 3813 (4), 3836 (10), 4042 (4), 3670 bis (19), 3671 bis (4); **Muniez, A. A.** 57 (14); **Muñoz** 1306 (19), 1405 (19), 1410 (32); **Muñoz Pizarro, C.** B-157 SGO 57745 (28a); **Muñoz, J. de D.** 1277 (32), 1313 (32), 1379 (21), 1380 (32); **Müsch, P.** 990 (27), 1021 (27); **Nájera, J.** 15 (4), 40 (29); **Naranjo, C.** 754 (32), 755 (19), 758 (19), 760 (19), 763 (32), 765 (19), 766 (27), 767 (27), 771 (29), 772 (32), 780 (32), 789 (29), 877 (18), 930 (9), 931 (9); **Navas, J. R.** 6 (3); **Nee, M.** 33656 (6), 33739 (6), 35333 (32), 35722 (6), 38987 (6), 39059 (6), 39732 (6), 40028 (6); **Negritto, M.** 388 (16); **Neiff, J.** 224 (25), 834 (25); **Neuman, R.** 394 (23); **Neumeyer, J. J.** 436 (3); **Nicora, E. G.** 138 (29), 140 (19), 141 (21), 147 (33), 200 (29), 543 (8), 653 (10), 811 (19), 873 (19), 971 (29), 1309 (33), 1312 (21), 1317 (29), 1471 (33), 1526 (2), 1558 (19), 1981 (29), 2007 (19), 2014 (29), 2276 (19), 2316 (21), 2317 (21), 2323 (33), 2358 (18), 2379 (33), 2432 (19), 2454 (33), 2493 (33), 2557 (33), 2593 (19), 2640 (19), 2774 (33), 2860 (29), 3279 (19), 3281 (29), 3285 (19), 3286 (19), 3290 (29), 3541 (32), 3542 (29), 4012 (9), 4248 (33), 4257 (21), 4351 (3), 4352 (18), 4568 (29), 4636 (29), 4664 (29), 4686 (29), 4758 (29), 4816 (2), 4817 (19), 4821 (2), 4956 (4), 6937 (8), 8142 (16), 8247 (16), 8295 (16), 8414 (18), 8469 (16), 8559 (16), 8569 (13), 8817 (16), 9756 (30), s.n. SI 17611 (19), s.n. SI 17640 (33), s.n. SI 17676 (33), s.n. SI 17724 (19), s.n. SI 17785 (33), s.n. SI 17834 (33), s.n. SI 17867 (29), s.n. SI 17911 (2), s.n. SI 18560 (32), s.n. SI 18625 (21), s.n. SI 19553 (18); **Niglia, A.** 4 (19); **Novara, L. J.** 506 (7), 835 (23), 2121 (19), 5623 (2), 5673 (6), 8244 (4), 9277 (19), 9403 (21), 9418 (19); **Novatis, H. S. de** s.n. BAB 70223 (17); **Nuñez, F.** 1187 (25); **Obregozo** 397 (7); **Ocampo, E.** 1429 (33); **O'Donell, C. A.** 340 (33), 493 (33), 610 (33), 893 (33), 1026 (3), 2237 (9), 4427 (33), 4467 (33); **O'Dwyer, E. B.** s.n. SI 26396 (14); **Offermam, C.** s.n. (9); **Olea, D.** 278 (19); **Olmstead, R.** 177 (3), 196 (5a), 2004-107 (29), 2004-108 (32), 2004-118 (4), 2004-122 (30), 2004-123 (19), 2004-124 (10), 2004-148 (18), 2004-149 (18), 2004-153 (9), 2004-156 (16), 2004-161 (18), 2004-172 (28a), 2004-183 (15), 2004-205 (15), 2007-5 (2), 2007-31 (16), 2007-58 (16), 2007-66 (19), 2007-70 (23), 2007-73 (7), 2007-84 (33); **Orbea, R.** s.n. SI 18724 (19), s.n. SI 18746 (18); **Osten, C.** 2748 (18), 5642 (24), 13571 (10), 19188 (21), 20754 (7); **Otto, A.** 6445 (5a), 8138 (5a), s.n. LP 12999 (9), s.n. LP 13520 (9); **Pabst, G.** 6093 (20); **Pagliari, E.** 804 (2); **Palacios, M. A.** 773 (20), 1920 (29), 4236 (33), 4267 (33); **Palarí** 749 (32); **Panigatti, A.** 572 (29); **Parker, H. L.** s.n. SI 25668 (24); **Parodi, D.** 61 (8), s.n. (8), s.n. (8); **Parodi, L. R.** 14066 (33), 14069 (33); **Pascoal, D.** s.n. HUI 4478 (19), s.n. HUI 4860 (19); **Pastore, A. I.** 136 (19), 148 (29), 361 (33), 723 (10), 1163 (29), s.n. SI 3572 (14), s.n. SI 984 (29); **Pastore, F.** 33 (19), 56 (21), 148 (29), 983 (14), 1163 (29), 1199 (19), 2006 (21), 2007 (19), 2035 (22), 2036 (19), 2038 (19), 2057 (21), 2075 (33), s.n. SI 1210 (21), s.n. SI 984 (29); **Pastrana** 9156 (7); **Pedelaborde, J. L.** 12099 (29), 12106 (19), 12174 (29); **Pedersen, T. M.** 4069 (17), 4262 (25), 4484 (30), 5234 (11), 5344 (25), 7171 (25), 9078 (10), 9134 (30), 9176 (29), 9238 (26), 9585 (19), 9627 (25), 9923 (33), 10188 (31), 11445 (24), 11580 (21), 11672 (32), 12388 (30), 12556 (17), 12592 (10), 12944 (30), 13292 (9), 13998 (17), 14829 (30), 15658 (21), 15908 (20), 16228 (21); **Pensiero, J.** 893 (32), 1395 (32), 1547 (27), 1702 (32), 1703 (29), 2838 (32), 3366 (29), 3499 (32), 4178 (19), 4308 (32), 4381 (6), 4510 (23); **Peña-Chocarro, M.** 1824 (10); **Peralta, M.** 106 (21), 107 (29); **Pereira, E.** 7689 (4); **Perez Moreau, R. A.** 3687 (33), s.n. BA 31/2243 (30); **Pérez Moreau, R. L.** 3038 (9), 3190 (9), 3278 (13), 3407 (9), 3687 (33); **Pérez, B.** 145 (19); **Pérez, L.** 285 (4), 2567 (4); **Perrone, V. R.** 30338 (3); **Petersen, E.** 57 (12); **Petrocelli, A.** 36 (9); **Pfister, A.** 7294 (3); **Philippi, F.** s.n. SGO 42486 (28a), s.n. SGO 42524 (28a), s.n. SGO 54740 (28a), s.n. SGO 68382 (28a); **Philippi, R. A.** s.n. (3), s.n. (3); **Piccinni, B.** 2022 (33), 2565 (19), 3850 (19); **Pieroth, S.** 72839 (4); **Pierotti, L.** s.n. LIL 100804 (6); **Pierotti, S. A.** 1223 (23), 4123 (17), 5152 (33), 6556 (6), s.n. (33), s.n. LIL 154762 (33), s.n. LIL 99460 (33), s.n. LIL 99587 (33), v 108 (33); **Pin, A.** 333 (10); **Pivetta** 977 (20), 968 PACA 59156 (19); **Poggio** 837 (32), 849 (29); **Porto, M. L.** s.n. ICN 9586 (19); **Pott, A.** 3866 (17), 6816 (4); **Pozner, R.** 193 (33); **Prado** 56 (29), 234 (29); **Prina, A.** 1203 (3), 1233 (3), 1341 (3), 1467 (3), 1520 (5b), 1569 (5b), 1743 (3), 2625 (3), 2635 (3), 2655 (3), 2700 (18); **Proyecto Ventania** 89 (21), 186 (21), 892 (21); **Pujalte, J. C.** 43 (14), 121 (16); **Quarín, C.** 513 (19), 655 (32), 1239 (19), 1240 (29), 1887 (32), 2124 (19), 2437 (30), 2642 (25), 2797 (10), 2863 (10), 3879 (32), 3881 (30); **Rabinovich, D.** 130 (19), 154 (29);

Ragonese, A. 9 (32), 49 (29), 2003 (29), 2042 (19), 2397 (19), 2606 (19), 2842 (19), 3007 (19), 3274 (19), 5006 (29), 8775 (18), 9404 (29), 9580 (29), 9616 (33), 9830 (33); **Rambo, B.** 444 (20), 9366 (26), 9950 (26), 32817 (20), 34719 (4), 37693 (20), 42606 (19), 43620 (10), 43780 (20), 51652 (4), 53317 (4), 53369 (17), 54059 (20), 55939 (20), 56245 (19), 59244 (20), s.n. PACA 444 (20), s.n. PACA 1120 (20), s.n. PACA 4488 (20), s.n. PACA 4561 (20), s.n. PACA 4775 (20), s.n. PACA 8513 (20), s.n. PACA 8781 (20), s.n. PACA 8990A (19), s.n. PACA 8999 (20), s.n. PACA 9118 (19), s.n. PACA 9165 (4), s.n. PACA 9544 (19), s.n. PACA 9958 (19), s.n. PACA 11262 (19), s.n. PACA 1137 (19), s.n. PACA 26992 (20), s.n. PACA 28579 (19), s.n. PACA 28583 (10), s.n. PACA 29550 (19), s.n. PACA 3038 (4), s.n. PACA 3042 (19), s.n. PACA 30980 (20), s.n. PACA 31723 (19), s.n. PACA 32817 (20), s.n. PACA 34719 (29), s.n. PACA 34729 (14), s.n. PACA 36417 (19), s.n. PACA 36419 (20), s.n. PACA 37345 (19), s.n. PACA 37498 (19), s.n. PACA 37693 (20), s.n. PACA 38555 (20), s.n. PACA 38753 (19), s.n. PACA 39020 (20), s.n. PACA 3939 (4), s.n. PACA 39592 (19), s.n. PACA 39810 (19), s.n. PACA 3982 A (14), s.n. PACA 4242 (29), s.n. PACA 4273 (20), s.n. PACA 42781 (19), s.n. PACA 42941 (19), s.n. PACA 42959 (4), s.n. PACA 43282 (19), s.n. PACA 43350 (20), s.n. PACA 4336 (20), s.n. PACA 43524 (19), s.n. PACA 43620 (20), s.n. PACA 43778 (29), s.n. PACA 43780 (20), s.n. PACA 44020 (20), s.n. PACA 44104 (29), s.n. PACA 44165 (20), s.n. PACA 44275 (19), s.n. PACA 46335 (19), s.n. PACA 51378 (29), s.n. PACA 52102 (14), s.n. PACA 52158 (20), s.n. PACA 53317 (4), s.n. PACA 54059 (20), s.n. PACA 54786 (19), s.n. PACA 55909 (19), s.n. PACA 55939 (20), s.n. PACA 56245 (19), s.n. PACA 56659 (20); **Ramirez, J. R.** 342 (32), RAP 338 (32); **Rasp, A. E.** 152 (3), 177 (9), 193 (18), 194 (18), 196 (18); **Rau, G.** s.n. SMDB 267 (19); **Raviolo** 7 (29); **Rea Clavijo, J.** 46 (16); **Reales, A.** 617 (7), 631 (7), 1444 (7), 1525 (7), 1922 (7), 1931 (7); **Reca, A. R.** 15 (16), 21 (16), 41 (16); **Reiche, K.** s.n. SGO 68376 (28); **Reitz, P. R.** 155 (19), 888 (19), 2233 (19), 4445 (32), 4523 (20), 10248 (20), 11306 (20), 11372 (20), 12526 (20), 13335 (20), 16941 (20), 6404a (20), C 882 (17), c1279 (29), c1279e (29), c1280e (HBR, LIL, SI) (29), c1281 (19), C1962 (19), c882 (19); **Renaudeau** 100 (19); **Rentzell, I. von** 1099 (27), 1100 (29), 1101 (21), 1102 (19), 18829 (33), s.n. SI 15231 (33); **Renvoize, S. A.** 2852 (19), 2853 (29), 3069 (11), 3111 (20), 3149 (11), 3414 (16), 3463 (23); **Ribas, O. S.** s.n. (29); **Ricardi, M.** 3939 (28a), 5689 (3); **Rimbach** 23 (9), s.n. LIL 31746 (9); **Rocha, R.** 482 (33), 1391 (33), 2339 (8), 2340 (19), 2437 (32), 2668 (4), 2880 (9), 3693 (19); **Rodríguez** 297 (22); **Rodríguez, F. M.** 19 (7), 30 (10), 55 (32), 297 (16), 530 (10), 548 (30), 576 (32), 578 (4), 657 (19); **Rodríguez, V.** 566 (14), 907 (19); **Roig, F. A.** 8151 (15), 8382 (15), 8908 (9), 13056 (3), s.n. (18); **Rojas, T.** 1882 (10), 1894 (17), 1895 (17), 2527 (25), 2528 (4), 2536 (4), 3395 (19), 3628 (25), 3864 (20), 4736 (10), 5891 (30), 7647 (17), 8374 (32), 8991 (25), 9011 (4), 11785 (30), 12111 (32), 12868 (30), 14061 (17), 14169 (25), 14395 (4), 4819a (19); **Romanczuk, C.** 126 (29), 418 (32), 718 (10); **Rosa, E. B.** 11 (33); **Rosengurtt, B.** 491 (25), 1004 (24), 1005 (21), 1006 (24), 1009 (21), 1015 (24), 1110 (25), 1428 (19), 2116 (24), 2133 (21), 2351 (25), 8593 (29), 8858 (11), 10484 (29), 21161/2 (8), B 2244 (32), b1012 (19), B-182 (24), b749 (19), B-8042 (11), B-810 (21), b891 (19), PE-5056 PACA 32950 (21), s.n. ICN 18829 (19), s.n. ICN 18830 (19); **Rosillo, M. A.** 23 (19); **Rossato, M.** 5346 (20); **Rossi, J. B.** 850 (33), s.n. LP 918399 (33); **Rossow, R.** 245 (13), 1518 (18), 4735 (14); **Roth** s.n. (5a); **Rotman, A. D.** 197 (33), 204 (2), 235 (2), 252 (2), 261 (19), 423 (16), 437 (33), 578 (7), 806 (6), 819 (6), 856 (21), 868 (19), 870 (7), 882 (7), 990 (2); **Royo Pallarés, O.** 222 (19); **Rua, I. de la** 76 (19); **Rúgolo, Z.** 832 (27), 1263 (21), 1268 (29); **Ruíz Huidobro, A. M.** 1176 (29), 1575 (21), 3079 (6); **Ruíz Leal, A.** 157 (13), 1167 (18), 1284 (22), 1507 (18), 3505 (3), 3627 (5a), 3628 (3), 4686 (3), 4825 (16), 5367 (3), 6913 (9), 6936 (9), 7093 (9), 7117 (9), 7468 (9), 7500 (9), 8497 (15), 8503 (9), 8556 (16), 8650 (3), 8960 (9), 9291 (9), 9455 (9), 9655 (9), 9790 (9), 15723 (5b), 21137 (33), 21162 (19), 21270 (16), 21343 (22), 21899 (33), 21945 (9), 22009 (5a), 22141 (28a), 22230 (15), 22276 (29), 22319 (29), 22326 (21), 23248 (16), 23482 (22), 23619 (28a), 24005 (13), 24324 (5a), 24337 (9), 24450 (3), 24515 (9), 25496 (18), 25505 (9), 25539 (13), 25582 (13), 25698 (5a), 25716 (5a), 25758 (13), 25911 (18), 26037 (29), 26039 (19), 26042 (18), 26196 (9), 26293 (32), 26323 (22), 26329 (22), 26357 (13), 26394 (13), 26605 (5a), 26715 (9), 26753 (3), 26853 (9), 27181 (15), 28142 (22), 7093a (9), s.n. (16); **Ruthsatz, B.** 163 (16), 203 (16), 226 (16), 239 (16), 297 (16); **Saa, J.** s.n. CONC 126799 (28a); **Salas, J. C.** s.n. (2); **Salgado, C.** 30 (19); **Sanchéz, M. I.** 300 (3); **Sanzin, R.** 132 (28a), 139 (33); **Saravia, E.** 993 (4); **Saravia Toledo, C.** 720 (7), 1405 (32), 2837 (19), 10599 (6), 10719 (23), 12899 (21), 12956 (19), 13117 (21), 14375 (23), 14622 (23); **Sayago, M.** 295 (21), 409 (21), 860 (21), 1470 (33), 1655 (33), 2132 (2), 2370 (19), 2511 (29), 2663 (33), 2683 (12); **Scala, A. C.** s.n. LP 8496 (14); **Scappini,** E. 1440 (33); **Schajovskoy, S.** 48 (3), 138 (9), 154 (3), 154/IV (3), 38/III (3), 44/IV (3), 45/IV (3), 49/III (9), 65/IV (3), 89/III (13), s.n. (9), s.n. SI 26740 (13); **Schinini, A.** 445 (32), 1200 (4), 1673 (4), 3489 (10), 4028 (4), 4449 (32), 4476 (29), 4664 (29), 5109 (32), 5111 (32), 5143 (29), 5251 (19), 6805 (19), 6824 (19), 7011 (4), 7012 (19), 8308 (19), 8832 (32), 8891 (32), 9224 (4), 9576 (19), 9672 (4), 9866 (19), 10300 (11), 10373 (30), 11123 (10), 11599 (32), 11600 (29), 11778 (30), 11866 (30), 12753 (4), 13002 (10), 13209 (30), 14102 (30), 14940 (19), 15408 (10), 15480 (30), 15732 (10), 15821 (10), 16587 (4), 18509 (10), 20861 (26), 20884 (25), 20898 (10), 21632 (19), 21821 (20), 24817 (19), 25241 (11), 25830 (4), 25846 (17), 25980 (10), 26070 (30), 27579 (10), 27597 (11), 28329 (25), 31285 (19), 31286 (29), 31287 (19), 31321 (30), 32979 (23), 35058 (25), 1DB (20); **Schnack, B.** 7 (22), 21 (9), 476 (6), s.n. SI 26401 (7), s.n. SI 26402 (27), s.n. SI 26403 (27), s.n. SI 26404 (9), s.n. SI 26406 (16), s.n. SI 26409 (30), s.n. SI 26410 (11), s.n. SI 26411 (27), s.n. SI 26412 (32), s.n. SI 26413 (32), s.n. SI 26414 (29), s.n. SI 26415 (33), s.n. SI 26416 (33), s.n. SI 26417 (27), s.n. SI 26689 (10); **Schreiter** 3821 (6), 5013 (7), 5149 (12), 5151 (19), 6620 (21), 6679 (19), 11128 (12), 11464 (23); **Schrottky, C. B.** 13 (30), 15 (4), 25 (14); **Schuask, B.** s.n. (14); **Schult** 464 (19), 466 (20), 702 (19); **Schulz, A. G.** 246 (32), 266 (4), 268 (4), 269 (26), 270 (17), 285 (25), 783 (32), 1468 (26), 1475 (32), 1476 (19), 2887 (19), 2888 (4), 2892 (21), 3988 (23), 5267 (23), 5299 (6), 5337 (6), 5680 (4), 5991 (21), 6469 (19), 6469 (17), 6581 (21), 6869 (19), 6894 (11), 7440 (32), 7815 (17), 7945 (30), 7989 (30), 8802 (25), 8835 (25), 8892 (4), 8926 (4), 8962 (32), 9098 (32), 9266 (2), 10034 (19), 11309 (17), 11456 (19), 16084 (25), 16321 (17), 16397 (17), 16593 (19), 17618 (17), 18691 (10), 18725 (10), 264 a (19), s.n. (19); **Schwabe, H.** 561 (33), 796 (16), 924 (16); **Scur, L.** 501 (19); **Sehnem, A.** 3698 (19), 3882 (19), 7256 (19), 10791 (20), 12443 (4), 17089 (20), 9197 C (19); **Seijo, G.** 1132 (23), 1383 (21), 1425 (9), 1448 (9), 1456 (9), 1745 (21), 1746 (19), 1747 (33), 1809 (33), 2153 (18), 2255 (3), 2672 (21); **Selander, R. B.** 88-A-7 (16); **Semper, J.** 4259 (3); **Shwarz** 789 (30); **Silva, J. M.** 3617 (4); **S. Coll.** 55 (23), 333 (8), 735 (19), 891 (29), 1044 (29), 1639 (15), 3420 (7), 4046 (29), 5856 (5a), 107 SI 28107 (6), 1969 SI 26407 (20), 6181 LIL 31349 (32), s.n. (16), s.n. (19), s.n. (4), s.n. (8), s.n. (9), s.n. (19), s.n. (19), s.n. (19), s.n. (32),

s.n. (3), s.n. (4), s.n. (18), s.n. (32), s.n. CONC 102860 (13), CNPO 1817 (20), s.n. CNPO 2865 (19), s.n. ICN 28852 (20), s.n. SGO 54747 (28a), s.n. SGO 42534 (15), s.n. SGO 54796 (15), s.n. SI 26401 (7), s.n. SI 3371 (29), s.n. SI 3379 (9), s.n. SI 3405 (15), s.n. SI 26419 (29); **S. H.** 614 (6); **Slanis, A.** 155 (12), 167 (19), 193 (33); **Sleumer, H.** 2694 (32), 3542 (12); **Smith, L. B.** 8478 (20), 10203 (10), 11638 (20), 12592 (20), 13223 (20); **Sobral, M.** 463 (4), 1718 (30), 2018 (4), 2668 (20), 3343 (21), 4439 (21), 6504 (20), 7697 (11), 8096 (20), 8981 (20), 9282 (29); **Solbrig, O.** 156 (19); **Solís Neffa, V.** 639 (6), 813 (21); **Solomon, L. C.** 9996 (23); **Sonego, R.** s.n. HUI 5297 (19), s.n. HUI 5299 (19); **Soriano, A.** 482 (21), 668 (16), 710 (7), 862 (19), 927 (19), 1314 (3), 2121 (13), 2146 (13), 2147 (13), 2148 (13), 2270 (13), 3217 (5a), 3416 (13), 3736 (13), 3872 (13), 4042 (9), 5049 (5a); **Soza, V.** 1813 (32), 1819 (6), 1830 (16), 1842 (33); **Spaholi, J.** 39248 (29); **Spegazzini, C.** 10216 (10), 10298 (29), 10336 (32), 10410 (19), 10445 (25), 10559 (7), 10768 (7), s.n. (10), s.n. (19), s.n. (29), s.n. (32), s.n. (8), s.n. (19), s.n. (19), s.n. (21), s.n. (32), s.n. (33); **Spies** s.n. PACA 37030 (19), s.n. PACA 63207 (29); **Stehmann, J. R.** 684 (19); **Steibel** 762 (29), 1059 (29), 3077 (9), 3363 (29), 3972 (18), 5167 (32); **Steinbach, J.** 2533 (4), 2673 (4); **Strehl, T.** 179 MPUC 638 (19); **Stuessy, T. F.** 6906 (13); **Sturzenegger, O.** BACP 2433 (17), BACP 2490 (17), s.n. BACP 3048 (4); **Sxur, L.** 157 (20); **Taylor, C. M.** 11459 (7); **Tell** s.n. (19); **Teodoro Luis, I.** 6 (ICN, SI) (19); **Terribile, M.** 157 (32), 366 (32), 448 (32), 476 (32), 492 (32), 739 (33); **Theissen** s.n. PACA 7848 (20), s.n. PACA 7850 (19), s.n. 25298 (20), s.n. PACA 25190 (19), s.n. PACA 25213 (19); **Tirel, C.** s.n. (22); **Titos** 770 (32); **Tivano** 644 (29), 644a (33); **Tolaba, J. A.** 1957 (19), 2312 (6), 3455 (6); **Tombesi, T. S.** 37 (33); **Torena, M.** 1010 (2); **Tórgo, F.** 21259 (19); **Torres, A.** 144 (20), 1017 (21); **Torres, B.** s.n. LP 918528 (16), s.n. LP 918537 (16); **Torres, F.** s.n. CONC 25157 (28a); **Torres, L. M.** 50 (9), 51 (28a); **Trelles, J.** 3352 (19); **Tressens, S. G.** 21 (19), 135 (32), 482 (10), 1713 (10), 1782 (30), 1874 (11), 1917 (26), 2677 (10), 3126 (25), 3819 (10), 4112 (10), 4113 (30), 4211 (25), 4362 (25), 6563 (10); **Troiani, H.** 3446 (19), 15021 (9), 15052 (13), 15107 (3), 15121 (9), 15813 (3), 15947 (5a); **Troncoso, N. S.** 128 (29), 170 (29), 172 (8), 179 (14), 190 (29), 201 (19), 291 (29), 318 (19), 386 (21), 1063 (29), 1157 (29), 1219 (29), 1441 (29), 1652 (29), 1690 (29), 1755 (2), 1775 (2), 1791 (33), 1855 (33), 1921 (33), 1966 (29), 2055 (29), 2080 (29), 2207 (29), 2346 (32), 2641 (27), 2651 (27), 2768 (29), 2978 (29), 3036 (19), 3335 (27), 3767 (4), 3868 (29), 6022 (29), 19528 (33), 19532 (33), 19535 (33), s.n. SI 17859 (29), s.n. SI 19530 (32), s.n. SI 20587 (21), s.n. SI 27089 (29), s.n. SI 27116 (29), s.n. SI 27689 (8), s.n. SI 27711 (29); **Ulibarri, E. A.** 623 (19), 916 (33), 1013 (2), 1384 (33), 1479 (16); **Ulibarri, U.** 1780 (4); **Umana, A.** 26 (10); **Urbani, M.** 76 (32); **V. Dellaméa, M.** 2939 (19); **Valencia, J.** s.n. SI 14924 (29), s.n. SI 14925 (19); **Valentini, A.** 47 (19), 501 (19), 503 (29); **Valla, J. J.** 18521 (3); **Vallerini, M. C.** 196 (3), 1488 (13), 1530 (13), 2080 (5a), 2156 (5a), 3571 (5a), 3630 (13), 3779 (5a), 3806 (13), 6339 (13); **Vanni, R.** 571 (10), 737 (19), 1203 (4), 1558 (19), 1573 (10), 1842 (4), 3041 (32), 3056 (10), 3856 (10), 4292 (19); **Varocca, J.** 17322 (23); **Vattuone, I. C.** 60 (14), 102 (19), 132 (21), s.n. (19); **Vavrek, D.** 287 (32); **Vegetti** 1006 (29); **Velho, A.** 16844 (20); **Venturi, S.** 4 (2), 14 (29), 378 (19), 1042 (2), 1930 (2), 2303 (2), 2651 (7), 2898 (7), 2922 (7), 3568 (12), 3579 (7), 3677 (33), 4063 (12), 4762 (2), 5027 (7), 5056 (23), 5132 (12), 5143 (21), 5264 (7), 5270 (19), 5329 (12), 7163 (2), 7164 (19), 7840 (33), 7976 (21), 8356 (12), 8777 (16), 9389 (16), 10752 (23), 14 (2da serie) (29), 33/6574 (32); **Vidal, M. I.** 44 (5a); **Vignati, M. A.** 158 (33), 196 (33), 289 (33), 290 (33), 524 (33), 592 (33), 969 (33), 7042 (21), 7066 (19), s.n. SI 14926 (16), s.n. SI 7060 (33), s.n. SI 7075 (15), s.n. SI 7077 (33), s.n. SI 7089 (15), s.n. SI 7089 (15), s.n. SI 7091 (21); **Villa, E.** 453 (32), 680 (32); **Villafane, M.** 323 (33); **Villagrán, C.** 7808 (3); **Villamil, C. B.** 2046 (21), 2146 (21), 2395 (21), 2398 (29), 2489 (29), 2573 (19), 2580 (21), 2585 (21), 2639 (29), 2725 (9), 3131 (19), 3155 (21), 3232 (9), 4348 (29), 4382 (19), 4422 (19), 4618 (29), 7131 (29); **Volponi, C. R.** 26 (13), 307 (28a), 360 (21), 377 (32), 592 (33); **von Ihering, H.** 373 SP 20071 (4); **von Rentzell, S.** s.n. SI 19219 (33); **Vuoto, P.** s.n. BACP 2049 (4); **Walmich, C.** 2244 (2); **Wasum, R.** 208 (19), 1178 (20), 1557 (20), 2042 (20), 2933 (19), 3298 (20), 6433 (19), 7391 (24), 8051 (20); **Werner, D.** 639 (16); **West, H.** s.n. LIL 281948 (7); **Wolf** 49 (32), 156 (4); **Woolston, A.** 306 (25), 731 (32); **Xifreda, C. C.** 343 (19), 5149 (19); **Zabala, S.** 285 (19); **Záchia, R.** 2749 (19), 2903 (19); **Zanhali** s.n. HAS 39248 (29); **Zardini, E. M.** 153 (21), 210 (8), 524 (19), 611 (29), 957 (4), 1145 (21), 2553 (4), 2730 (19), 3071 (19), 5359 (32), 6930 (4), 7115 (32), 7486 (30), 10808 (4), 13380 (32), 13773 (32), 14196 (4), 14217 (32), 14283 (32), 14534 (32), 14586 (32), 14887 (32), 15293 (32), 15564 (32), 15957 (19), 16127 (4), 16149 (25), 16237 (4), 16240 (32), 16417 (4), 16447 (4), 16685 (32), 16877 (32), 17202 (32), 17366 (4), 17441 (4), 17443 (4), 18128 (32), 18260 (32), 18567 (10), 18598 (4), 18633 (4), 18674 (32), 18836 (4), 19239 (32), 19999 (32), 20155 (19), 21312 (32), 21564 (32), 21774 (19), 22127 (32), 22263 (4), 22491 (4), 22773 (32), 22899 (4), 22901 (32), 22968 (32), 22972 (4), 23020 (32), 23024 (4), 23099 (32), 23186 (10), 23255 (32), 23317 (4), 23388 (32), 23389 (4), 23448 (32), 23543 (4), 23571 (4), 23577 (32), 23824 (32), 24191 (4), 24201 (32), 24322 (4), 24439 (32), 24442 (4), 24533 (4), 24649 (30), 24654 (19), 24823 (19), 24939 (4), 24943 (4), 25053 (4), 25333 (4), 27284 (32), 27646 (32), 27692 (32), 29395 (19), 58589 (19), 58674 (32), 58679 (11), 58696 (4), 59129 (4), 59148 (20), 59221 (10), 59380 (19), 59482 (29), 59727 (29), 59866 (4), 59910 (32), 59970 (19), 60255 (19), 60286 (19); **Zöller, O.** 5417 (13); **Zuloaga, F. O.** 589 (10), 645 (19), 646 (30), 968 (19), 1016 (11), 1254 (19), 1637 (23), 2321 (29), 2509 (7), 2565 (23), 2662 (7), 2726 (6), 3120 (29), 3252 (10), 3308 (30), 3649 (7), 3653 (7), 3662 (19), 4556 (6), 4912 (11), 5779 (19), 6012 (16), 6054 (16), 7625 (7), 7884 (19), 7888 (2), 8099 (4), 8103 (30), 8393 (4), 8420 (2), 9108 (12), 9161 (16), 9415 (2).

CARACTERÍSTICAS ANATÓMICAS DE HOJA Y FLOR CON IMPORTANCIA TAXONÓMICA PARA LA DELIMITACIÓN DE CUATRO ESPECIES EN EL GÉNERO *MOUSSONIA* (GESNERIACEAE)[1]

Angélica Ramírez-Roa[2] *y Gerardo Varela Hernández*[3]

Resumen

La falta de un tratamiento taxonómico y de claves de determinación en el género *Moussonia* Regel (Gesneriaceae) ha propiciado que algunas especies sean confundidas entre sí o que se les haya considerado como variedades o sinónimos. Además, varios caracteres morfológicos y anatómicos no han sido evaluados para ayudar a distinguir especies en *Moussonia*. En este trabajo nos enfocamos principalmente en varias características anatómicas del envés de la hoja y del mesófilo, así como de la epidermis de la superficie adaxial del tubo de la corola. Estos caracteres resultaron tener valor taxonómico para delimitar cuatro especies incluídas en *Moussonia*: *M. ampla* L. E. Skog, *M. deppeana* (Schltdl. & Cham.) Hanst., *M. elegans* Decne. y la nueva combinación *M. jaliscana* (S. Watson) D. L. Denham ex Ramírez-Roa, transferida de *Isoloma jaliscanum* S. Watson. En este estudio observamos características anatómicas de las hoja tales como domos estomatales generalmente con uno o dos estomas en la cresta, tamaño relativo y densidad aparente de los estomas, células epidérmicas que rodean la base de tricomas, tipo de tricomas en el envés de la hoja, anatomía del mesófilo, y variaciones de las paredes anticlinales y periclinales de las células de la superficie adaxial de la corola. Discutimos brevemente algunas posibles interpretaciones de esta anatomía con relación al ambiente. Presentamos un breve tratamiento taxonómico de las especies revisadas en este trabajo para un mejor entendimiento de la problemática subyacente. Considerando características anatómicas y morfológicas proponemos una nueva definición de *M. elegans*, junto con los cambios nomenclaturales correspondientes. Incluimos una nueva combinación: *M. jaliscana* y una clave de determinación usando caracteres anatómicos y morfológicos.

Abstract

The lack of a taxonomic treatment and keys for the genus *Moussonia* Regel (Gesneriaceae) has led some species to be confused with each other or to be considered as varieties or synonyms. Additionally, several morphological and anatomical characters have not been evaluated for their usefulness in discriminating *Moussonia* species. In this work we focus principally on the study of several morphological and general anatomical features of the abaxial surface of the leaf and of the mesophyll as well as the adaxial surface of the corolla tube. We found that these features have taxonomical value to delimit four species included in *Moussonia*: *M. ampla* L. E. Skog, *M. deppeana* (Schltdl. & Cham.) Hanst., *M. elegans* Decne., and the new combination *M. jaliscana* (S. Watson) D. L. Denham ex Ramírez-Roa, as transferred from *Isoloma jaliscanum* S. Watson. Anatomical features of the leaf such as stomatal domes generally with one or two stomata on the top, relative stomata size, epidermal cells surrounding

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trichome bases, trichome types, apparent density of stomata and trichomes on the leaf lower surface, blade mesophyll, and variation of epidermal cells on the adaxial surface of the corolla were observed. We briefly discuss some possible interpretations of this anatomy with respect to the environment. A brief taxonomic treatment of the species considered in this work is included for a better understanding of the underlying problem. Considering these anatomical and morphological features, we propose a new definition of *M. elegans*, together with the corresponding nomenclatural changes. We propose *M. jaliscana* as a new combination and include an identification key using anatomical and morphological features.

Key words: Anatomy, Gesneriaceae, *Moussonia*.

El género *Moussonia* Regel pertenece a la tribu Gloxinieae Fritsch, subfamilia Neotropical Gesnerioideae, familia Gesneriaceae (Burt & Wiehler, 1995; Skog & Boggan, 2006). Regel (1847) describe por primera vez al género que es reconocido posteriormente por Decaisne (1849), Walpers (1849), Oersted (1861) y Hanstein (1854, 1865). Sin embargo, Hemsley (1882) lo considera como sinónimo de *Isoloma* (Benth.) Decne y Fritsch (1893–1894) lo incluye como una sección del género *Kohleria* Regel tomando en cuenta casi exclusivamente semejanzas morfológicas externas de la flor (Ramírez-Roa & Chiang, 2010). Aunque Morton (1938, 1967) y Gibson (1974) reconocen la combinación de Fritsch, Wiehler (1975a) reestablece al género *Moussonia* considerando diferencias morfológicas y del cariotipo, como el hábito leñoso, ausencia de rizoma, nectario anular, estigma estomatomorfo, y $n = 11$. Wiehler (1975a) también evalúa la incapacidad de producir híbridos fértiles entre las especies de ambos géneros y reconoce once especies para *Moussonia*.

Desde la re-circunscripción taxonómica de Wiehler (1975a), *Moussonia* se mantiene como un género aparte (Skog, 1976, 1978a; Kvist y Skog, 1992; Burtt & Wiehler, 1995; Skog & Boggan, 2006; Ramírez-Roa, 2007a, 2007b; Weber & Skog, 2007; Ramírez-Roa & Chiang, 2010). Análisis moleculares de marcadores nucleares y del cloroplasto, y estudios morfológicos apoyan el reconocimiento del género como un grupo monofilético que comprende 12 especies (Roalson et al., 2005a, 2005b).

Actualmente, estudios morfológicos han apoyado la extensión de *Moussonia* a 14 especies (Ramírez-Roa, 2007b). La mayoría de las especies del género se distribuyen desde el norte de México hasta Guatemala (Morton, 1967; Wiehler, 1975a; Skog, 1978b; Ramírez-Roa, 2007a), y cuatro se reportan solamente para Centroamérica (Morton, 1938, 1939; Standley & Williams, 1952; Skog, 1979). Sin embargo, la autora estima que el número de especies incluidas en *Moussonia* es mayor. Estudios de herbario e inventarios florísticos en progreso sugieren que alrededor de 19 especies están presentes en México y Guatemala, y que cinco especies son posiblemente endémicas a Centroamérica. Estos estudios además sugieren a México como el centro de origen y principal centro de diversificación de *Moussonia* y de otros taxa de la familia como *Achimenes* Pers., *Smithiantha* Kuntze y *Solenophora* Benth (Ramírez-Roa & Skog, datos no publicados).

Moussonia se reconoce por el hábito leñoso, cimas generalmente umbeladas con tres a cuatro flores, flores tubulares y ventricosas de color rojo o rojo anaranjado, ovario semi-ínfero, estigma estomatomorfo, nectario anular, y el fruto capsular cortamente rostrado. Tradicionalmente, la delimitación de sus especies se ha basado en el número de flores presentes en las inflorescencias y características de la flor (forma general de la corola, forma de los lóbulos del cáliz, color de la corola, etc.), pero ocasionalmente también se utiliza la forma de la hoja y el tipo de indumento. El número reducido de características que normalmente se consideran en la taxonomía del grupo, la falta de evaluación taxonómica de otros caracteres morfológicos y anatómicos para la delimitación de especies, y la carencia de claves de determinación, ha propiciado que algunas especies sean confundidas entre sí. *Moussonia deppeana* (Schltdl. & Cham.) Hanst. a pesar de presentar varias discontinuidades morfológicas se confunde frecuentemente con *M. elegans* Decne. Incluso por la sola semejanza de la forma de la corola y color de las flores y la forma de las hojas algunas especies se han reducido a sinonimia, como en el caso de *Kohleria papillosa* (Oerst. ex Hanst.) Fritsch (Fritsch, 1913; Morton, 1967) ahora incluida en *M. elegans* (Wiehler, 1975a).

La sobre simplificación de los caracteres diagnósticos llevó a incluir en *Moussonia elegans* seis especies distintas y tres variedades como sinónimos heterotípicos (Fritsch, 1913; Morton, 1967; Gibson, 1974; Wiehler, 1975a; Kvist & Skog, 1992), esta especie presenta la mayor variación morfológica dentro del género. Si bien los taxones comprendidos en esta especie son relativamente parecidos por sus corolas tubulares rojas o rojo-anaranjadas, otros caracteres morfológicos y anatómicos sugieren que por lo menos siete de ellos son realmente especies distintas. La amplia variación morfológica atribuida a *M. elegans* s.l., tanto en la hoja, cáliz, corola, inflorescencia, etc., ha contribuido a dudar en el

reconocimiento de algunos otros taxones que llegan a coincidir en algunas características de esta especie, como *M. deppeana* (Skog, com. pers.). Además, se ha observado que ejemplares de herbario que en realidad representaban especies nuevas fueron inicialmente determinados como *M. elegans*, debido a que no podían ser ubicados fácilmente dentro de otras especies del género (Ramírez-Roa, 2007a, 2007b).

Este trabajo está enmarcado en la revisión taxonómica que la autora realiza para el género. La examinación morfológica detallada de especies descritas hasta el momento y de especies aceptadas como sinónimos heterotípicos, mostró diferencias significativas tanto en caracteres morfológicos como anatómicos. Estos estudios indican que la apariencia general de la superficie del envés, la presencia de domos estomatales generalmente con un estoma en la cresta y el tamaño relativo de estomas al menos en las especies estudiadas, son variables entre especies pero constantes dentro de cada especie, por lo que sería recomendable usarlos como una evidencia más para discriminar especies.

Los objetivos del trabajo son: 1) demostrar que algunas características de la epidermis tienen valor taxonómico en la delimitación de especies en el género *Moussonia*; 2) con la ayuda de estas evidencias redefinir a *M. elegans*; y 3) resaltar la utilidad de estos caracteres en la elaboración de descripciones y claves de determinación.

Antecedentes

La epidermis y sus derivados han sido caracteres importantes para describir, unir, o separar grupos taxonómicos en Gesneriaceae (Esau, 1965; Metcalfe & Chalk, 1972; Fahn, 1978; Mauseth, 1988). En la familia es conocido el gran valor taxonómico del caracteres como: el tipo de tricomas, su presencia o ausencia, y densidad y ubicación en la planta (Denham, 1949; Wiehler, 1970, 1975b, 1983; Metcalfe & Chalk, 1972; Skog, 1976), la distribución de estomas (aislados o agrupados), la presencia de domos estomatales, y la forma de las células epidérmicas (Wiehler, 1970, 1975b, 1983; Skog, 1976, 1978a; Beaufort-Murphy, 1983; Kvist & Skog, 1989). La variación de estos caracteres ha apoyado la separación de especies de un género o reunión de taxa en grupos de rango taxonómico superior, como en el caso de las tribus Gesnerieae y Nepeantheae (Wiehler, 1970, 1983) o el género *Gasteranthus* Benth. Este género previamente incluido en *Besleria* L. (Wiehler, 1975b) es ahora re-validado al nivel genérico por la presencia de estomas agregados, entre otros caracteres.

El impacto en la sistemática y taxonomía de Gesneriaceae de los caracteres anatómicos previamente mencionados y los morfológicos, explica su uso reiterado en descripciones de géneros y especies de la familia (Denham, 1949; Wiehler, 1970, 1975b, 1983; Skog, 1976; Ramírez-Roa, 1987; Kvist & Skog, 1989, 1992, 1993, 1996; Smith, 1994; Skog & Kvist, 2000; Ramírez-Roa & Skog, 2002; Weigend & Förther, 2002; Ramírez-Roa, 2007a, 2007b; Rodríguez-Flores & Skog, 2008; Ramírez-Roa et al., 2009). Algunos estudios en Gesneriaceae han incluido micrografías de microscopía electrónica de barrido que muestran los caracteres anatómicos con mayor detalle y belleza, y Skog (1978a) explica claramente las ventajas, posibilidades e importancia de hacer estudios en las gesneriáceas utilizando este tipo de microscopía.

Wiehler (1970, 1983), después de revisar varias tribus de la subfamilia Neotropical Gesnerioideae, a la cual pertenece *Moussonia*, reporta que los domos estomatales son característicos de las tribus Gloxinieae y Gesnerieae y están ausentes en la subfamilia Coronanthoideae. En relación a la anatomía de los domos estomatales, explica que estas estructuras generalmente presentan uno o dos estomas en la parte superior del domo, que se forman por la separación y elevación tanto de las células epidérmicas adyacentes al estoma como de las propias células subsidiarias, en zonas localizadas, por arriba del parénquima esponjoso, y que siempre se distribuyen en el envés de las hojas. También observó que las células epidérmicas en el domo son típicamente más pequeñas que el resto de las células epidérmicas. En sus estudios, Whieler (1979, 1983) indica la posible correlación entre la presencia de domos estomatales con ambientes húmedos y plantas terrestres con hojas delgadas, pubescentes.

Por otro lado, en relación a los tricomas, Wiehler (1979, 1983) menciona que los tricomas glandulares uniseriados, son más o menos raros en la subfamilia, señalando dos tipos principales. El primer tipo se constituye basalmente por un pie de células largas y delgadas y apicalmente por una glándula de una o varias células, que al tocarla se rompe y deja salir su conteniendo, un líquido de color anaranjado-amarillento. El otro tipo de tricoma con forma de hongo tiene en la base una o dos células cortas y anchas y hacia el ápice una glándula de una a varias células. Los tricomas glandulares largos los encontró en varias partes de la planta y los tipo hongo, en la superficie de las hoja o principalmente en la superficie adaxial de la garganta de la corola y estilo.

Skog (1976), en su estudio sobre la tribu Gesnerieae, reporta e ilustra la presencia de domos estomatales y la morfología de tricomas no glandulares. Para *Rhytidophyllum tomentosum* (L.) Mart. describe tricomas no glandulares uniseriados y simples, rodeados en la base por un anillo de células epidérmicas largas que no se observan en los tricomas glandulares. Uno de los aspectos importantes incluidos en el trabajo de Skog (1976), es la posible interpretación ecofisiológica de la anatomía de las especies en relación al ambiente. Este autor indica que en *Rhytidophyllum* Mart., los domos estomatales más altos se encuentra en especies densamente pubescentes, que ocupan taludes expuestos y secos o en claros del bosque. Con base en estas observaciones, Skog (1976) sugiere que los domos estomatales permiten una transpiración más eficiente en el microclima húmedo que se crea en el indumento denso de la superficie del envés. Las interpretaciones de Skog (1976) se contraponen con las de Wiehler (1970), quien correlacionó los domos estomatales con ambiente sombreados, o con las de Haberlandt o Biebl y Germ, quienes correlacionan los domos estomatales con hábitats sombreados y húmedos (revisado en Skog, 1976).

Por otro lado, Skog (1976), con base en observaciones en *Gesneria* L., indica que la intensidad de luz podría determinar el número de capas celulares en el mesófilo y la diferenciación del parénquima en empalizada y del tejido esponjoso. Este autor reporta, que en plantas de *G. exserta* Sw. creciendo en áreas al descubierto y en pleno sol, observó un mesófilo claramente diferenciado en un parénquima en empalizada grueso, compuesto de uno a tres substratos celulares y un tejido esponjoso definido por varios substratos de células isodiamétricas. Por el contrario, en plantas de *G. reticulata* (Griseb.) Urb. poco expuestas a sol directo, Skog (1976) observó una sola capa de parénquima en empalizada y una o dos capas de tejido esponjoso.

Kvist y Skog (1992), en su revisión del género *Kohleria*, describen algunas características anatómicas del haz y del envés de la hoja que ilustra con micrografías del microscopio electrónico de barrido (MEB). En este estudio los autores reportan los dos tipos de tricomas glandulares mencionados por Wiehler (1983) y los domos estomatales. Además, indican que los domos estomatales más altos se encontraron en plantas con indumento denso, y explican que la elevación de los estomas en domos estomatales facilitan el proceso de transpiración, al permitir que los estomas se ubiquen por arriba de la capa de aire y humedad, la cual no se mueve debido al indumento. Previos estudios en *K. spicata* (Kunth) Oerst., especie que vive en hábitats con exposición solar directa, muestra domos bien desarrollados contrastando notoriamente con los domos bajos de las especies del género que crecen en condiciones de sombra. Kvist y Skog (1992) mencionan que aunque entre las especies del género el indumento es variable, dentro de cada especie la variabilidad es constante.

Rodríguez-Flores y Skog (2008) al revisar el género sudamericano *Corytoplectus* Oerst., utilizan la coloración del haz de las hojas como uno de los caracteres distintivos del género y diferencias en los tipos de tricomas e indumento para delimitar especies. De hecho, en su revisión taxonómica del género, la clave de determinación de especies, comienza precisamente con las diferencias en el indumento del haz de las hojas. Posteriormente, Ramírez-Roa et al. (2009) al describir la primera especie no sudamericana (endémica de México) de *Corytoplectus*, confirman la importancia y utilidad del tipo de indumento y la superficie de la hoja para incorporar la especie en el género y reconocer su afinidad con otras especies. Además, muestran las primeras imágenes del haz y el envés de la hoja en el género.

Tanto Denham (1949) como Wiehler (1983) llegan a la conclusión de que el tipo de tricomas en las gesneriáceas no varían dentro de una misma especie, por lo que se pueden usar estas características para distinguirlas. Sin embargo, encontraron que el ambiente puede influir en la densidad y distribución de ellos en los órganos de la planta.

En lo que se refiere a las especies del género *Moussonia*, existen pocos trabajos en donde se mencionan las características de la epidermis y sus derivados. Uno de ellos es la tesis doctoral de Miriam Denham (1949) en donde la autora hace una revisión de literatura sobre los tricomas, y menciona solamente a *M. deppeana* y *M. elegans*. Denham (1949) menciona que Weiss en 1867 describe los tricomas de la primera especie como uniseriados, puntiagudos (señalados como típicos en la familia Gesneriaceae), con la base del tricoma bulbosa parcialmente sumergida en un collar de células epidérmicas, y tricomas glandulares pequeños con una célula en el eje y con dos a cuatro células en la cabeza, las cuales secretan una sustancia ligeramente aromática. Denham (1949), señala que en *M. elegans* las terminaciones celulares de los tricomas están abruptamente alargadas y, como consecuencia, se ven geniculadas.

Otro trabajo que presenta datos sobre la anatomía de la epidermis de *Moussonia*, es la tesis doctoral de Hans Wiehler (1970), publicada en 1983. Este autor esquematiza la epidermis de los domos estomatales y

estomas de *M. deppeana*, *M. elegans* y *M. hirsutissima* (C. V. Morton) Wiehler, y un tricoma glandular con el pie y las células epidérmicas adyacentes en *M. elegans* (Wiehler, 1983: 92–93, figs. 176, 182–183) y señala que, *M. deppeana* y *Kohleria tubiflora* (Cav.) Hanst., presentan los domos estomatales más altos y un mesófilo con el parénquima esponjoso y el de empalizada claramente diferenciados (Wiehler, 1983: 99, fig. 213). Wiehler (1983: 92–93, figs. 176, 182) muestra que en *M. deppeana* y *M. elegans* el envés de las hojas tiene domos estomatales muy evidentes. Para *M. elegans* Wiehler (1983: 99, fig. 213) ilustra un tricoma no glandular con un pie uniseriado con una de tres células, siendo la última, puntiaguda, y en la base alrededor del tricoma seis células epidérmicas que elevan al tricoma sólo un poco por arriba del nivel general de la epidermis. Las células de la base del tricoma, sólo se diferencian del resto de las células epidérmicas, por ser un poco más grandes y planas. Sin embargo estas células son diferentes en géneros como *Columnea* L. (sección *Dalbergaria* Tussac, tribu Episcieae), *Kohleria*, *Achimenes* Pers. y *Capanea* Decne. de la tribu Gloxinieae (Wiehler, 1983: 92–99, figs. 91, 93, 214–215), en donde son mucho más grandes que el resto de las células epidérmicas, largas y de apariencia redondeada y turgentes.

Por último, Ramírez-Roa (2007a, 2007b) ha señalado las diferencias en la superficie del haz y envés de las hojas, tipos de tricomas y células en la base del pie de los tricomas, presencia de domos estomatales, y diferenciación del parénquima en empalizada en algunas especies de *Moussonia* como *M. adpressipilosa* D. L. Denham ex Ramírez Roa, *M. hirsutissima*, *M. larryskogii* Ramírez-Roa y *M. strigosa* (C. V. Morton) Wiehler. Ramírez-Roa ha incluido, en sus estudios del género, claves de identificación que utilizan las características morfológicas y anatómicas previamente discutidas. Estos caracteres han sido útiles para reconocer tanto a las especies de *Moussonia* ya mencionadas, como a *M. ampla* L. E. Skog, *M. elegans*, *M. rupicola* (Stand. & L. O. Williams) Wiehler, *M. serrulata* (C. V. Morton) Wiehler, *M. fruticosa* (Brandegee) Wiehler y *M. viminalis* (Brandegee) Wiehler.

Materiales y Métodos

Las especies que se incluyeron en este estudio fueron seleccionadas tomando en cuenta los siguientes criterios: 1) que pudieran mostrar la variación de los caracteres anatómicos conocida hasta el momento para el género *Moussonia*; 2) incluir a las dos especies con problemas de delimitación, *M. deppeana* y *M. elegans*; 3) mostrar las posibles diferencias entre una de las especies con amplia sinonimia, *M. elegans* y *M. jaliscana* (S. Watson) D. L. Denham ex Ramírez-Roa comb. nov. [= *Isoloma jaliscanum* S. Watson] uno de sus sinónimos.

Las observaciones preliminares y generales se hicieron exclusivamente en ejemplares de herbario, utilizando microscopio de disección (MD), con el objeto de reconocer los caracteres que por su constancia, pudieran servir para la delimitación de las especies aquí estudiadas. De todos los ejemplares de herbario observados, sólo se indican algunos representativos de cada taxón, los cuales están citados en las descripciones correspondientes que se incluyen más adelante.

Una vez reconocidos los caracteres anatómicos y morfológicos que se tomarían en cuenta para cada especie, se procedió a tomar las muestras para las observaciones anatómicas en el MEB, con el fin exclusivamente de aumentar la resolución de las observaciones, observar con más facilidad las estructuras, y complementar su descripción. Los ejemplares estudiados con el MEB, provienen de la colección del Herbario Nacional de México (MEXU), y fueron los siguientes: *Moussonia ampla* (Panamá. *Van der Werff 7255*, MEXU-250256), *M. deppeana* (Veracruz, México. *Ventura 18120*, MEXU-751039), *M. elegans* (Chiapas, México. *Breedlove 48663*, MEXU-778741) y *M. jaliscana* (Jalisco, México. *Pringle 11072*, MEXU-29588).

Las muestras para ser observadas al MEB fueron tomadas en la parte media de hojas maduras, recortando dos rectángulos aproximadamente de 2 × 2 mm a partir del margen hacia la vena media, con el fin de tener representado tanto el haz como el envés. De la corola en antesis se tomaron porciones equivalente en tamaño, ubicadas cerca de la garganta y hacia la base de la corola con el fin de observar la superficie adaxial y abaxial de la corola, tanto en la parte dorsal como en la ventral. Las muestras fueron directamente montadas para su observación en MEB, cubiertas con oro, y observadas en un MEB marca Hitachi S-2660N (Tokio, Japón). Las medidas se reportan en micrómetros.

El material de herbario observado en MEB no fue hidratado, considerando que ayudaría más el ver en las micrografías los tricomas, estomas y células en general tal como se observarían con el microscopio de disección. Además como es sabido el trabajo taxonómico y el uso de las claves se realiza, la mayoría de las veces, con material de herbario, esto es, deshidratado. La terminología morfológica se

realizó siguiendo el glosario botánico ilustrado de Moreno (1984).

Resultados

Las observaciones en MD, incluyen tanto los caracteres morfológicos como los anatómicos. Los caracteres morfológicos serán presentados en las descripciones al final de este trabajo, mientras que los anatómicos se reportan a continuación.

Los resultados en MD incluyen observaciones de varios ejemplares de herbario, los cuales se enlistan, en su totalidad o parcialmente en cada una de las descripciones según sea el caso. Cabe mencionar que las características anatómicas observadas en MD pueden ser vistas a simple vista. Los caracteres anatómicos observados incluyen: epidermis del envés de la hoja y la superficie adaxial de la corola. En el envés de la hoja se observó el relieve de la superficie, domos estomatales, tipo y densidad aparente de tricomas, células en la base de los tricomas y células epidérmicas adyacentes, y densidad aparente de estomas. Además, se estudio la anatomía del mesófilo caracterizando parénquima esponjoso y tejido en empalizada con el grosor relativo de la lámina foliar. En la superficie adaxial de la corola se consideró la forma y superficie de las células epidérmicas.

Envés de la hoja

Relieve. En observaciones en MD y MEB se reconocieron tres tipos de relieve de la superficie del envés. El primero se denominó relieve plano o más o menos plano, presente en *Moussonia deppeana* y *M. elegans* (Fig. 1A, B). El segundo se denominó relieve ampollado, siguiendo la denominación de Skog (1976), en este tipo con base en observaciones de MD, la superficie presenta pequeños abultamientos esponjosos a manera de ampollas o papilas, que se distribuyen muy cerca unas de otras. Estos abultamientos son aun más evidentes en MEB (Fig. 1C) y son característicos de *M. ampla*. El tercer tipo se denominó relieve sinuoso, en el que la superficie es ondulada como en *M. jaliscana* (Fig. 1D).

Domos estomatales. En el relieve ampollado los estomas se distribuyen sobre los domos estomales que son abultamientos altos y anchos, estos se pueden apreciar con toda claridad en MD. En este relieve el espacio entre la epidermis y el parénquima esponjoso al elevarse y formarse el domo estomatal es muy evidente (Fig. 2B). El relieve plano contrasta con el relieve ampollado por presentar los domos estomatales reducidos como máculas, esto es, bajos y estrechos, ocupando el espacio casi exclusivamente del estoma (Fig. 2A, B), siendo ligeramente elevados en *Moussonia elegans* y más evidentes en *M. deppeana*. En este relieve la separación de la epidermis del tejido esponjoso es poco evidente (Fig. 2A). Por el otro lado en el relieve sinuoso, los domos no se limitan al estoma como en el relieve casi plano, pero tampoco se encuentran bien delimitados como un abultamiento como en el relieve ampollado, más bien se aprecian como ondulaciones en donde los estomas se encuentran en la parte superior de los abultamientos (Fig. 1D). La separación de la epidermis del mesófilo en el relieve sinuoso es semejante al que se aprecia en la Figura 2A.

Mesófilo. En la hoja de *Moussonia ampla* el mesófilo se encuentra bien diferenciado en una capa de parénquima en empalizada hacia el haz y de tres a cuatro capas de parénquima esponjoso formado por células irregularmente cúbicas a irregularmente esféricas hacia el envés (Fig. 2B). La separación del parénquima esponjoso de la epidermis por debajo del domo estomatal es muy evidente. En las otras especies sólo se observa claramente definido el parénquima esponjoso con células más o menos rectangulares (Fig. 2A). A excepción de *M. ampla* con hojas ligeramente coriáceas, el resto de las especies incluidas en este estudio tienen hojas relativamente delgadas, lo cual se podría explicar por la reducción de número de capas celulares en el mesófilo.

Tricomas y células epidérmicas adyacentes. Las células epidérmicas alrededor de la base de los tricomas pueden ser semejantes al resto de las otras células de la epidermis (Fig. 1B, C), o alternativamente más largas que las células epidérmicas adyacentes, perfectamente turgentes y con las paredes periclinales redondeadas (Fig. 1D). Estas diferencias se observan claramente tanto en MD como en MEB. El número de células alrededor de la base de los tricoma varia entre las especies de *Moussonia* de cinco en *M. jaliscana* a ocho o nueve células en el resto de las especies.

En cuanto a tipo de tricomas, se presentan tres tipos. El primero es el tricoma glanduloso, el cual es delgado y largo, con un anillo de células epidérmicas en la base, esta presente solamente en *Moussonia ampla* (Fig. 1C). En MD estos tricomas se aprecian delgados y largos con la glándula evidente; y con ayuda del MEB se ve perfectamente el pie de dos células de largo y la glándula en el ápice. El segundo tipo es el tricoma glanduloso tipo hongo, que en MD se observa como una esferita amarillenta muy pequeña. Este tipo se distribuye en toda la superficie

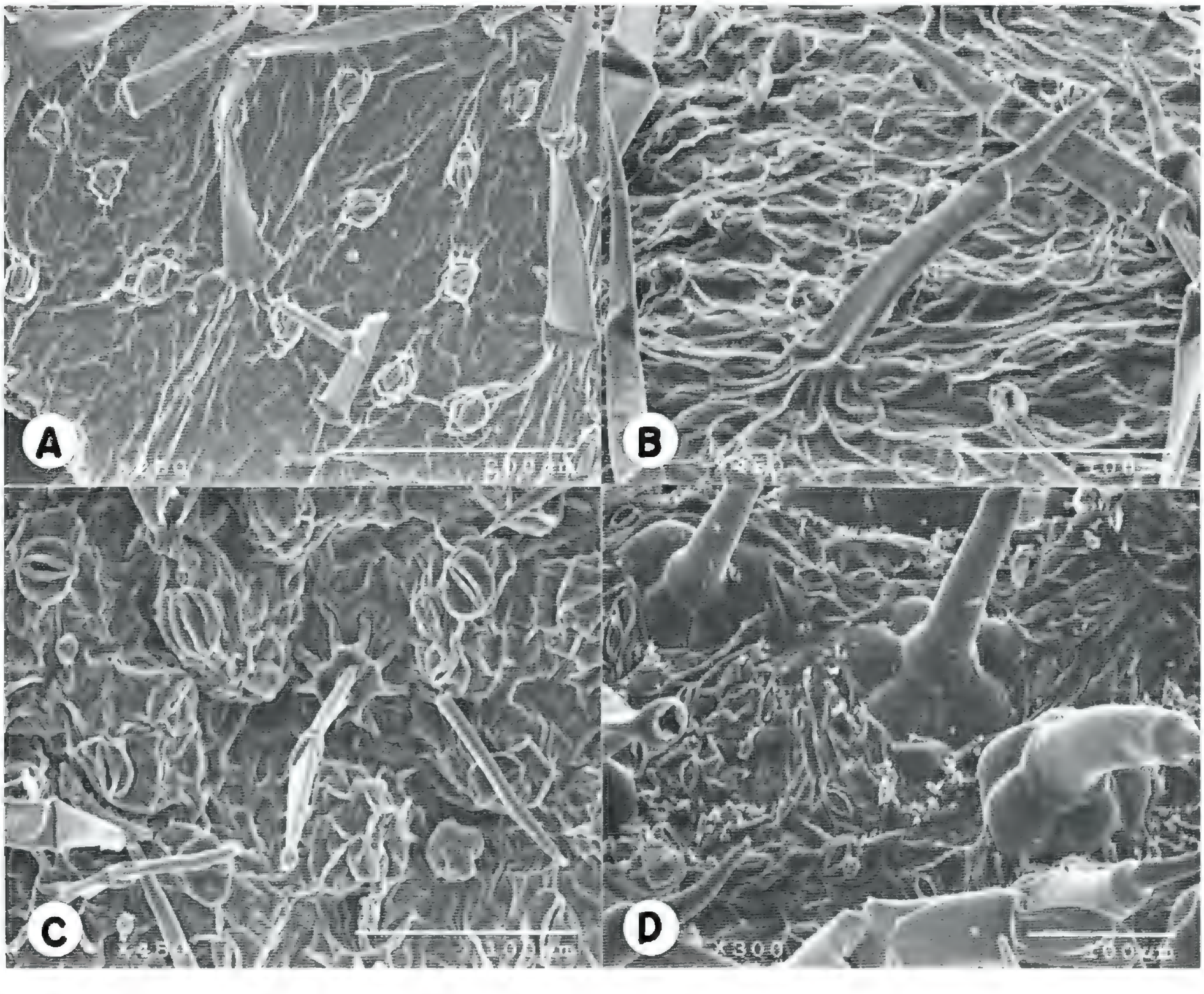

Figura 1. Envés de la hoja: tipo de relieve y domos. —A. *Moussonia deppeana*, relieve casi plano, estomas solo ligeramente elevados por los domos estomatales casi planos. —B. *M. elegans*, relieve y estomas como el anterior. —C. *M. ampla*, relieve ampollado, estomas elevados evidentemente, ubicados sobre los domos en forma de ampollas; tricoma uniseriado glandular al frente y dos tricomas tipo hongo del lado izquierdo, observándose de ellos solo la glándula o la glándula con el pie. —D. *M. jaliscana*, relieve sinuoso, estoma sobre las ondulaciones. A de *Ventura 18120* (MEXU 751039); B de *Breedlove 48663* (MEXU 778741); C de *van der Werff 7255* (MEXU 250256); D de *Pringle 11072* (MEXU 29588).

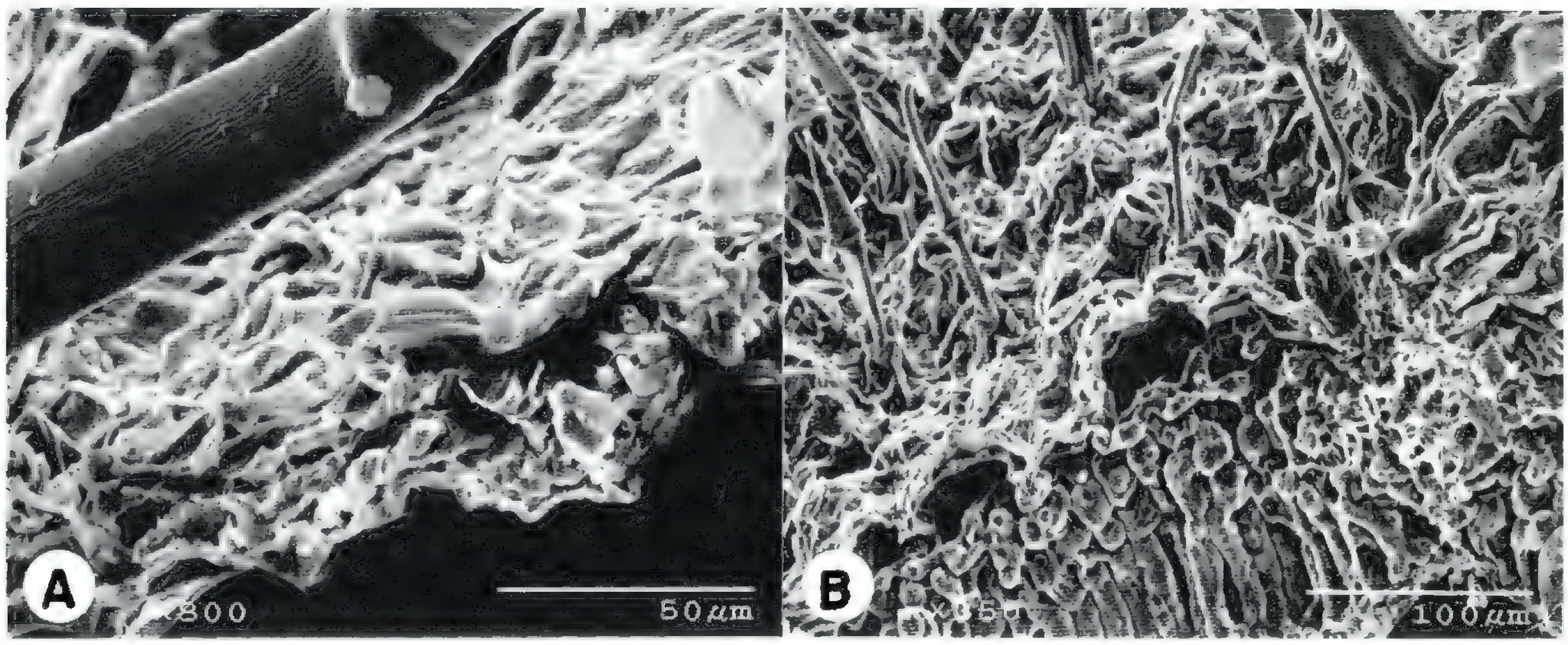

Figura 2. Corte transversal de la hoja. —A. *Moussonia elegans*, separación de la epidermis del envés del parénquima esponjoso, a la altura del domo estomatal, poco evidente; no se aprecia claramente el parénquima en empalizada. —B. *M. ampla*, separación de la epidermis del envés del parénquima esponjoso, a la altura del domo, muy evidente; parénquima en empalizada presente. Epidermis del envés hacia arriba, epidermis del haz hacia abajo, mesófilo entre las capas de epidermis, de la A de *Breedlove 48663* (MEXU 778741); B de *van der Werff 7255* (MEXU 250256).

de la hoja, pudiéndose confundir con partículas de cera y en ocasiones, no son fáciles de reconocer. En todos los taxa revisados en este trabajo bajo el MEB se observaron las cabezas de estos tricomas las cuales son mucho más pequeñas que las células de los estomas (Fig. 1C del lado izquierdo). El tercer tipo es el tricoma no glandular con varias células en el pie y la punta aguda, el cual se presenta en todas las especies excepto en *M. ampla*.

Densidad aparente de tricomas y estomas y tamaño preliminar de los estomas. Las especies con relieve plano muestran una menor densidad aparente de tricomas (Fig. 1A, B) que las especies con relieve ampollado o sinuoso (Figs. 1D, 2B). En lo que respecta a los estomas, también se observaron diferencias muy evidentes entre las especies, pero no dentro de cada especie. Por ejemplo, en *Moussonia deppeana* los estomas en MD se aprecian como "montículos amarillentos" muy evidentes, los cuales están densamente arreglados en la superficie; apreciándose incluso las células oclusivas y los ostiolos en algunos casos. Por el contrario en *M. elegans* la densidad aparente de estomas es menor y los estomas, se ven más bien como pequeñas máculas blanquecinas, laxamente distribuidos. En *M. jaliscana*, con relieve sinuoso, se aprecia la cercanía de los estomas de manera evidente, mientras que en *M. ampla* los estomas se distribuyen sobre el domo estomatal, observándose en algunos casos las células oclusivas y los ostiolos. Observaciones y medidas en MEB indican que *M. deppeana* y *M. ampla* presentan el mayor y el menor número de estomas por área, respectivamente, mientras que *M. elegans* y *M. jaliscana* muestras una densidad de estomas intermedia. La generalidad de este reporte sin embargo debe corroborarse con un la observación de un muestreo más amplio. En cuanto al tamaño de los estomas, *M. deppeana* tiene los estomas más grandes que son de apróx. 40 μm, mientras que *M. ampla* son de apróx. 28.12 μm, en *M. elegans* apróx. 26.29 μm, y se observan los estomas más pequeños en *M. jaliscana* con apróx. 24 μm.

SUPERFICIE ADAXIAL Y GROSOR DE LA COROLA

En MD los contornos de las paredes anticlinales de las células epidérmicas se aprecian más o menos claros mientras que en las paredes periclinales pueden ser papilosas proyectándose como muy pequeñas protuberancias sin distinguirse mayor detalle. Cabe mencionar que la corola puede ser translúcida cuando el grosor de la corola es delgada, como en *Moussonia ampla* o no translúcida si la corola es gruesa como en las demás especies.

Con base en MEB se describen cuatro tipos de células epidérmicas, que se describen considerando las variaciones morfológicas de las paredes anticlinales y periclinales de las células: 1) células con paredes anticlinales formando polígonos irregulares, organizadas densamente y con paredes periclinales papilosas (Fig. 3A); 2) células con paredes anticlinales formando rectángulos irregulares y paredes periclinales lisas (Fig. 3B); 3) células con paredes anticlinales formando polígonos irregulares—con cinco o seis lados y paredes periclinales lisas (Fig. 3C); y 4) células con paredes anticlinales formando polígonos irregulares y paredes periclinales con una protuberancia angular—proyección tipo pico curvo (Fig. 3D).

Moussonia jaliscana y *M. deppeana* muestras diferentes tipos celulares en la porción dorsal y ventral del tubo de la corola. En *M. jaliscana* la parte dorsal muestra el tipo celular 1 y la parte ventral el tipo celular 3 mientras que *M. deppeana* dorsalmente presenta el tipo celular 3 y ventralmente el tipo celular 4. En contraste *M. ampla* y *M. elegans* tanto dorsal o ventralmente sólo tienen el tipo celular 2 y 3, respectivamente.

DISCUSIÓN

ENVÉS DE LA HOJA

Superficie del envés, domos estomatales y mesófilo. Las especies examinadas son arbustos terrestres de hojas generalmente delgadas y pubescentes, que se establecen en húmedos de montaña o en encinares húmedos. Debido a la escasa información de las etiquetas de campo, es incierto si estas especies crecen sobre laderas sombreadas y húmedas o en laderas expuestas y secas. De acuerdo con Wiehler (1983), especies con hojas de indumento denso que ocupan lugares sombríos y húmedos presentan domos estomatales en la superficie del envés. De las especies estudiadas, *Moussonia deppeana* y *M. elegans* tienen hojas con indumento denso y presentan domos estomatales, aunque no los más altos. Contrariamente, *M. ampla* con los domos estomatales más evidentes muestra hojas con un indumento menos denso y un mesófilo con parénquima esponjoso y empalizada bien definidos y grueso. Aunque las características morfológicas de *M. ampla* corresponden con la descripción de Skog (1976) y Kvist y Skog (1992) para especies que se establecen en ambientes más expuestos, se desconoce si la especie vive en áreas sombrías o expuestas. Sin embargo otros estudios indican que la ilumina-

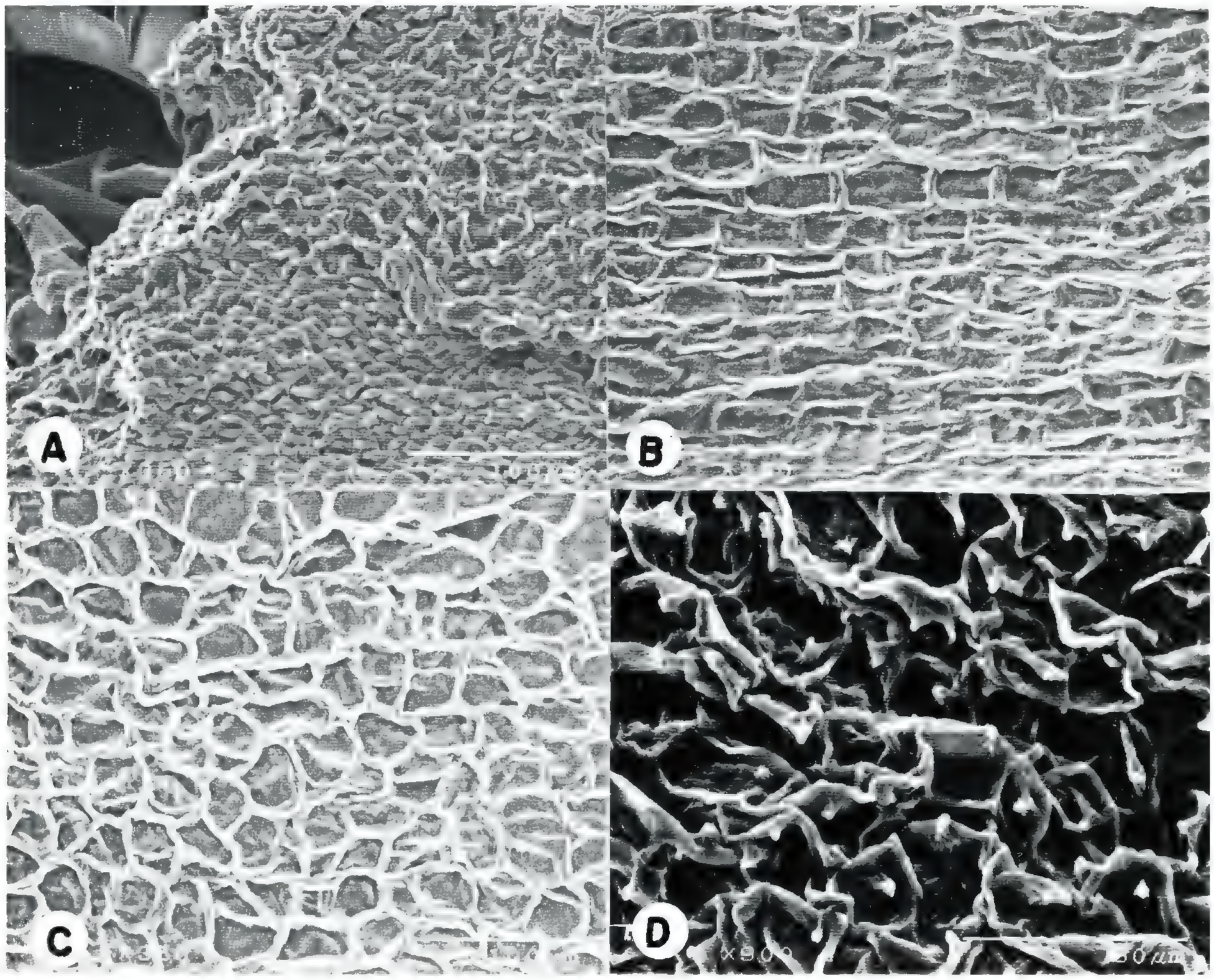

Figura 3. Superficie adaxial de la corola: forma de las células epidérmicas y superficie. —A. *Moussonia jaliscana*, paredes celulares anticlinales poligonales e irregulares, paredes celulares periclinales papiladas. —B. *M. ampla*, paredes anticlinales rectangular y paredes periclinales celulares lisas. —C. *M. deppeana*, paredes anticlinales de forma irregularmente poligonal, paredes periclinales lisas. —D. *M. deppeana*, con pliegue curvo. A de *Pringle 11072* (MEXU 29588); B de *van der Werff 7255* (MEXU 250256); C y D de *Ventura 18120* (MEXU 751039).

ción intensa y deficiencia hídrica podría aumentar el grosor del tejido en empalizada, seguramente determinando el incremento de la actividad fotosintética (Fahn, 1978).

Observaciones directas en el campo sugieren que cambios de humedad asociados a diferentes tipos de vegetación, podría estar influyendo más en las dimensiones del domo estomatal que la sola incidencia solar como menciona Skog (1976). Esta situación podría estar ocurriendo en *Moussonia larryskogii* y *M. hirsutissima* (Ramírez-Roa, 2007b). Ambas especies generalmente ocupan laderas protegidas en ambientes con diferentes regímenes de humedad, *M. larryskogii* caracterizada por el envés casi plano crece en bosque tropical perennifolio (vegetación con altos niveles de humedad), mientra que *M. hirsutissima* con domos estomatales evidentes crece en bosque húmedo de montaña es decir en una vegetación con menos húmeda que la anterior. Cabe aclarar que aunque las dos especies pueden encontrarse entre los dos tipos de vegetación en zonas de transición, aparentemente mantienen sus características anatómicas.

Aquí se reconocieron diferencias anatómicas y morfológicas útiles para distinguir *Moussonia deppeana* de *M. elegans*, sin embargo, estos caracteres son informativos siempre y cuando se consideren ambas especies en sentido estricto. Las características morfológicas que este par de especies pudieran tener en común se explica por la ambigüedad para definir los límites morfológicos de *M. elegans*, problema que se atribuye a la amplia variación morfológica asociada con la circunscripción de *M. elegans*, al incluir varias especies en sinonimia (Wiehler, 1975a). A continuación se presentan los caracteres anatómicos útiles para la distinción de estas dos especies.

Los domos estomatales de *Moussonia deppeana* son muy visibles tanto en MD como a simple vista, están relativamente juntos unos de otros, ocupando toda la superficie de la hoja, y presentan un color verde-amarillento. En *M. elegans* los domos estomatales son de menor tamaño y por lo tanto son menos evidentes

que los de *M. deppeana*. Además los domos estomatales en *M. elegans* estan dispersamente distribuidos y son de color verde pálido, tal como el envés. Al comparar el envés de las hojas en ambas especies en el MEB, *M. deppeana* presenta los domos estomatales más grandes y más densamente distribuidos. Considerando características macromorfológicas, las especies también se pueden distinguir fácilmente, *M. deppeana* tiene un indumento velutino, en varias partes de la planta, incluyendo la corola, los lóbulos de la corola son rectos y los lóbulos del cáliz son deltados a triangulares, mientras que *M. elegans* en sentido estricto, tiene un indumento viloso-piloso, corola laxamente pilosa con los lóbulos expandidos y lóbulos del cáliz lanceolado subulados.

También se observó que la caracterización de domos y mesófilos previamente descritos para *Moussonia deppeana* y *M. elegans* por Wiehler (1983), difiere de la nuestra. Nuestros estudios indican que los domos estomatales para *M. deppeana* ilustrados por Wiehler (1983, fig. 176) se parecen más a los que aquí reportamos para *M. ampla*. Similarmente es ese trabajo, el mesófilo observado para *M. deppeana* difiere de nuestras observaciones, Whieler (1983) presenta para esta especie un mesófilo con el parénquima en empalizada y esponjoso bien diferenciado con múltiple capas, mientras que nosotros observamos un mesófilo con el parénquima de pocas capas celulares, distinguiéndose sólo con certeza, el tejido esponjoso. En cuanto a *M. elegans*, Wiehler (1983) muy probablemente pudo haber observado domos altos en alguna de las especies que él consideraba como sinónimos. Por último, aquí reportamos diferencias entre *M. elegans* y *M. jaliscana* una de las especies incluidas en su sinonimia. En el envés de la hoja, el relieve plano de *M. elegans*, los domos estomatales planos y los estomas grandes ayudan a distinguirla de *M. jaliscana*. Además, la primera especie tiene, en la superficie adaxial de la corola células con paredes periclinales lisas y la corola ampliada, mientras que en la segunda las paredes son papilosas y la garganta de la corola es evidentemente constreñida, entre otras características.

TRICOMAS Y CÉLULAS EPIDÉRMICAS ADYACENTES

Moussonia elegans y *M. jaliscana* también se diferencian por los tricomas y las células alrededor de la base de los tricomas, la primer especie presenta en la base del tricoma un anillo de ocho a nueve células con paredes periclinales lisas y la segunda, un anillo de cinco células con paredes periclinales turgentes. Además, observaciones en MD, indican que en *M. jaliscana* las células en la base del tricoma presenta un contenido blanquecino, probablemente calcio, así como cera en forma de pequeñas esferas irregulares en la superficie del envés.

El tipo de tricoma puede utilizarse para separar *Moussonia ampla*, quien tiene tricomas del tipo 1, largos con glándula apical, del resto de las especies aquí estudiadas. Wiehler (1983) mencionó que este tipo de tricoma no es común en la familia. Nosotros agregaríamos que tampoco en el género, pues solo *M. rupicola* y *Kohleria papillosa* var. *pendula* C. V. Morton (= *Moussonia*) los presentan. Por el contrario, los tricomas tipo hongo al parecer son ampliamente distribuidos en el género, observándose diferencias en el tamaño y en la densidad relativa en la lámina de la hoja.

DENSIDAD APARENTE DE TRICOMAS Y ESTOMAS Y TAMAÑO DE LOS ESTOMAS

Existe aparentemente una correlación entre tricomas más o menos espaciados y el relieve casi plano con domos estomatales pequeños, como en *Moussonia deppeana* (Fig. 1), o entre alta densidad de tricomas y domos estomatales altos característicos de los relieves sinuosos o tipo ampolla, como en *M. jaliscana* y *M. ampla*, respectivamente (Fig. 2B). Estas observaciones apoyan la hipótesis de Skog (1976) que propone que la presencia de estomas en domos estomatales altos es una estrategia para efectuar una traspiración más eficiente, especialmente en plantas con un número elevado de tricomas. De acuerdo con Skog (1976) entre más denso el indumento más altos los domos estomatales. Sugerimos adicionalmente que el plegamiento de la epidermis al formar los domos estomatales consecuentemente también incrementa la densidad de tricomas por unidad de área y la humedad en la capa del indumento.

El tamaño de los estomas permite distinguir a *Moussonia deppeana* de *M. elegans*, y *M. elegans* de *M. jaliscana*. Tamaños de estomas y conteos estomáticos parecen ser buenos criterios para distinguir especies dentro del género.

SUPERFICIE ADAXIAL DE LA COROLA

Las células de la superficie adaxial de la corola pueden considerarse como otro criterio para separar las incluidas en este trabajo. Las modificaciones de las paredes periclinales de las células epidérmicas, como son las papilas encontradas solo en *Moussonia jaliscana* y los pliegues en *M. deppeana*, ayudan a separar estos taxones de *M. elegans*.

El grosor de la corola y la forma de las células epidémicas no habían sido reportados antes de este

estudio, sin embargo observaciones de material de herbario muestran que pueden ser caracteres útiles para distinguir especies. Podemos definir las corolas en seco como gruesas y no traslucidas, y delgadas y translúcidas en diferentes grados. Una de las corolas más gruesas en el género parece ser la de *Moussonia deppeana* y una de las más delgadas es la de *M. ampla*. La corola de la última especie es tan delgada que a través de ella se puede observar las siluetas de los estambres y estilo, estas estructuras son imposibles de observarse en especies con corolas gruesas como aquellas de *M. deppeana*. Es importante señalar que las observaciones hechas en material fresco en algunas especies del género, como en *M. deppeana*, *M. hirsutissima*, *M. larryskogii* y *M. triflora* (M. Martens & Galeotti) Hanst., confirman observaciones realizadas en material seco, al menos en los que se refiere al grosor y textura de las corolas. Corolas definidas como gruesas y no translucidas en seco, en fresco son gruesas y resistentes, por el contrario, corolas delgadas y translúcidas en seco son delgadas y frágiles en fresco. Se podría esperar que al comparar corolas gruesas y delgadas se presenten diferencias en las células epidérmicas, lo cual puede llegar a ser otro criterio que ayude a diferenciar especies en el género.

CONSIDERACIONES FINALES

Tal como Denham (1949), Skog (1978a, 1979) y Wiehler (1983) lo reiteran en su momento para otros géneros de gesneriáceas, en este trabajo se confirma la importancia de las células epidérmicas y sus derivados como criterios importantes para delimitar, en esta ocasión, especies en el género *Moussonia*. Aunque en general, los criterios anatómicos no son apreciables a simple vista (a diferencia de las corolas, la inflorescencia y las hojas), con la ayuda de un microscopio de disección se pueden reconocer sin mucho problema, tal como se hace al observar estructuras de flores muy pequeñas.

Aunque en este trabajo se analizaron básicamente los domos estomatales, la base de los tricomas y las células del interior de la corola, otras características de la epidermis y sus derivados, proporcionarán sin lugar a duda mayor información para la delimitación de las especies, tal como, número de células que conforman a los tricomas, color de esta células, resina o cualquier otra sustancia presente en el interior de los tricomas, tipo de estoma y número por área, indumento tanto en el haz como en el envés, etc.

Como se mencionó al principio de este trabajo, la información obtenida tiene como propósito ayudar a la delimitación de las especies. Por ello, se incluye una clave de determinación con las observaciones hechas en MD, las descripciones morfológicas, y la discusión taxonómica correspondiente para cada especie.

Clave de Determinación para las Cuatro Especies del Género *Moussonia* Incluidas en Este Estudio

1a. Envés de la hoja plano o casi plano, esto es, con los domos estomatales poco evidentes; hojas membranosas, suaves al tacto.
  2a. Estomas grandes, densamente distribuidos, ocupando casi completamente la superficie de la hoja, de color amarillento; corolas ventricosas, con la garganta constreñida, gruesas; lóbulo del cáliz triangular ..... 2. *M. deppeana*
  2b. Estomas pequeños distribuidos laxamente en la superficie de la hoja, de color blanquecino; corola ventricosa, ampliada hacia el limbo; lóbulo del cáliz lanceolado lineal ..... 3. *M. elegans*
1b. Envés de la hoja ampollado, esto es, con los domos estomatales evidentes, o con ondulaciones; hojas ligeramente coriáceas, rugosas al tacto.
  3a. Flores solitarias; hoja con el envés ampollada; base de los tricomas del envés con las paredes periclinales planas ..... 1. *M. ampla*
  3b. Flores en cimas; hoja con el envés ondulado; base de los tricomas del envés con las paredes periclinales de las células redondeadas ..... 4. *M. jaliscana*

Tratamientos Taxonómicos

1. Moussonia ampla L. E. Skog, Brittonia 30: 322. 1978. TIPO: Panamá. Prov. Chiriquí: 8 km W of Cerro Punta in vic. of Las Nubes, 11 Feb. 1978, *K. Utley 5670* (holotipo, US no visto; isotipos, DUKE no visto, MO!, MICH!).

Arbustos de 1 m de alto, con tricomas glandulares en varias partes de la planta, amarillos. Hojas ligeramente anisófilas, lanceoladas, ovado-lanceoladas o lanceolado-elípticas, de 7.5–13 × 2.7–5.2 cm, margen con 47 a 53 dientes desiguales, venas laterales 10 a 12; pecíolos 1.3–3.9 cm; haz más o menos papiloso, verde obscuro, base de los tricomas multicelular; envés ampollado, verde-amarillento, células epidérmicas alrededor de la base de los tricomas semejantes a las células adyacentes; domos estomatales altos muy evidentes en toda la superficie, distribuidos de manera relativamente densa, un estoma por domo; mesófilo claramente diferenciado en parénquima esponjoso y en empalizada. Flores solitarias; pedúnculos de 0.65–1.3 cm; brácteas florales frecuentemente caducas, 2–2.2 × 0.2 mm, lineares, vilosos, con tricomas glandulares; pedicelos delgados, 3.7 cm de largo, pilosos, rojizos, con tricomas glandulares; cáliz con el tubo obcónico, 3.5–

3.8 × 2–4.2 mm, lóbulos de 1.3–1.7 × 1–2 mm, linear-triangulares, margen dendroide hacia el ápice, cada lóbulo con diferente número de prolongaciones, verdes, pilosos por fuera y por dentro; corola tubular, ± ventricosa, constreñida por arriba de la base y en la garganta, 4.2–4.8 cm de largo, 1.2–1.3 cm de ancho en la garganta, 7–11 mm de ancho en la base, roja-anaranjada, laxamente pubérula por fuera, papirácea y más o menos translucidas en material seco, glabra por dentro, con células epidérmicas de la superficie adaxial con las paredes anticlinales irregularmente rectangulares y las periclinales lisas; lóbulos amplios, 4–6 × 7–9.5 mm, suborbiculares, crenados, ± expandidos; filamentos 3.5 cm de largo, base amarilla, seríceos, glabros hacia el ápice, anteras 2 × 2 mm, connatas en antesis, incluidas en la corola, estaminodio de 5 mm de largo; nectario de 0.5 mm de alto; ovario densamente piloso, estilo 4 cm de largo, piloso, incluido en el tubo de la corola. Cápsula no se observó.

Esta especie es conocida solamente de Panamá, en algunos cerros ubicados en la provincia de Chiriquí. Se encuentra en bosque mesófilo sobre taludes, algunas veces junto a cuerpos de agua, a una altitud de 1700–2100 m. Los ejemplares de herbario revisados indican la floración en febrero y mayo.

La especie se distingue por los tricomas glandulares presentes en varias partes de la planta, por el envés ampollado, las flores solitarias, el margen de los lóbulos del cáliz dendroide, las corolas ampliadas hacia el limbo y los lóbulos más o menos expandidos, con el tubo de la corola más o menos translúcido en seco y laxamente puberulento.

Por sus características peculiares *Moussonia ampla* es distinta a las otras especies del género. Sin embargo, la presencia de domos estomatales en el envés de las hojas lo comparte principalmente con *M. strigosa*, una especie de Costa Rica (Ramírez-Roa, 2007b). La escasa recolecta disponible para esta especie no permite por el momento conocer la variabilidad real del taxón.

Ejemplares examinados. PANAMA. **Chiriquí:** Cerro Pate Macho, trail from Rio Palo Alto, 4 km NE of Boquete, *Sytsma et al. 4834* (US); Cerro Pando, Santa Clara, Distr. Bugaba, *van der Werff 7255* (MEXU).

2. Moussonia deppeana (Schltdl. & Cham.) Hanst., Linnaea 34: 284. 1865. Basiónimo: *Gesneria deppeana* Schltdl. & Cham., Linnaea 5: 110. 1830. *Isoloma deppeanum* (Schltdl. & Cham.) Hemsl., Biol. Cent.-Amer., Bot. 2 478. 1882. *Kohleria deppeana* (Schltdl. & Cham.) Fritsch, Nat. Pflanzenfam. [Engler & Prantl] 4(3b): 179. 1894. TIPO: México. Veracruz, "in sylvis Jalapensibus," Oct., *C. J. W. Schiede 186* (lectotipo, designado por Ramírez-Roa & Chiang [2010: 298–299], HAL!; duplicado del lectotipo, OXF!).

Arbustos de 0.50–2.5 m de alto, velutinos en varias partes de la planta, con tricomas amarillentos o rojizos. Hojas generalmente anisófilas, lanceoladas a elíptico-lanceoladas, las grandes de 8–21 × 3.2–7.5 cm, las pequeñas de 7–12 × 2.5–5 cm, margen irregularmente dentado generalmente de 30 a 53 dientes, venas laterales 10 a 12; pecíolos 3.5–4.5 cm; haz verde obscuro, células epidérmicas alrededor de los tricomas semejantes a las adyacentes; envés ± plano, verde-amarillento, domos estomatales ligeramente elevados, distribuidos de manera relativamente densa, un estoma por domo; mesófilo donde solamente se distingue claramente el parénquima esponjoso. Cimas umbeladas de 4 flores; pedúnculos de 3.5–4.5 cm de largo; brácteas foliosas evidentes, elípticas pecioladas de 6–8 × 1.5–2 mm; pedicelos 2–2.5 cm de largo; cáliz con el tubo obcónico-triangular, 3–3.5 × 2–3.5 mm, lóbulos de 2.5–3.5 × 3–3.5 mm, deltados a triangulares, márgenes rectos, verdes, pilosos por fuera y por dentro; corola tubular, ventricosa, constreñida por arriba de la base y de la garganta, ligeramente ampliada hacia el limbo, 2.3–2.7 cm de largo, 0.6–1.2 cm de ancho en la garganta, 4–6 mm de ancho en la base, roja a rojo-anaranjada, densamente vilosa por fuera con tricomas rojizos, no translucida en material seco, glabra por dentro, con células epidérmicas de la superficie adaxial irregularmente poligonales y paredes periclinales lisas o con un pequeño pliegue en forma de pico curvo, lóbulos cortos, 2.5–2.7 × 3.5–3.8 mm, oblongos, crenados, más o menos rectos; filamentos 2.4–2.6 cm, puberulentos, anteras 1.5 × 1.5 mm, connatas en antesis, con algunos tricomas en la base del dorso, un estaminodio de 0.3 mm; nectario de 0.5 mm de alto; ovario densamente piloso, estilo 2.1–2.6 cm, piloso, exerto. Cápsula de 0.9–1.1 × 0.5–0.6 cm, ± esférica, las venas prominentes, pardo claro en material seco; semillas 0.4 mm, pardo-rojizas.

La especie se encuentra en México, en los estados de Guerrero, Hidalgo, Puebla, Oaxaca y Veracruz. En Guatemala se ha colectado en la Provincia de San Marcos. Se establece generalmente en bosque húmedo de montaña, algunas veces en encinar, raramente en pinar, a una altitud de 1180–1600 m. Florece generalmente de noviembre a mayo (información disponible en los ejemplares de herbario revisados).

Moussonia deppeana se distingue por la pubescencia densa de color amarillento principalmente en hojas, tallos, pedúnculos y pedicelos, por el envés de las hojas más o menos liso con domos cortos, muy

evidentes y en gran número, un estoma por domo, por las flores en cimas umbeladas de cuatro flores, brácteas foliosas evidentes, lóbulos del cáliz deltados a triangulares, de márgenes rectos y por las corolas ventricosas, rojas o rojo-anaranjadas, gruesas, no translúcidas, densamente rojo-velutino con los lóbulos más o menos rectos.

Esta especie se parece a *Moussonia skutchii* (C. V. Morton & D. N. Gibson) Wiehler, distinguiéndose ésta última principalmente por el color verde-olivo generalizado de la planta, el envés con la superficie generalmente ondulada y los estomas del color de la lámina, las brácteas obovadas, los lóbulos del cáliz ovado-triangular con los márgenes cóncavos, corolas con el tubo ampliado y los lóbulos expandidos.

Aunque en este trabajo solamente se está incluyendo un ejemplar por estado, se han hecho observaciones en más de 100 ejemplares depositados principalmente en: BM, ENCB, IEB, INEGI, MICH, MO, NY y US, encontrándose en general poca variación.

Skog (com. pers.) considera que esta especie y *Moussonia elegans* tradicionalmente han sido difíciles de distinguir por su parecido en la flor. Fritsch (1913) y Gibson (1974) señalaron que en Guatemala estas especies son simpátricas, encontrando especímenes con características intermedias. Fritsch agrega que las formas intermedias o híbridos son imposibles de determinar. En este trabajo no se descarta la posibilidad de formas intermedias, sin embargo, la forma de las hojas y su pubescencia tan característica, así como la forma y pubescencia de la corola y de los lóbulos del cáliz presentes en *M. deppeana*, no se encuentran en *M. elegans* s.l., menos aún en *M. elegans* s. str.

Ejemplares representativos. GUATEMALA. **Depto. San Marcos:** vic. Sibinal, *Steyermark 35956* (F). MÉXICO. **Guerrero:** San Antonio a Buenos Aires, *Hinton et al. 14031* (NY). **Hidalgo:** El Texme, 4.5 km O de Tenengo de Doria, camino a El Zotoy, *Alcántara 1583* (MEXU). **Puebla:** 6 mi. below Tezuitlan on Nautla rd., *Crutchfield & Johnston 5219* (MEXU, MICH). **Oaxaca:** 90–100 km SW of Sola de Vega, along rd. to Puerto Escondido, *Breedlove 62045* (MEXU). **Veracruz:** Plan de Cedeño, mpio. Acajete, *Ventura 18120* (MEXU, MO).

3. Moussonia elegans Decne., Fl. Serres Jar. Eur. 5: 489, tab. sin número, en la página anterior a la 489. 1849. *Isoloma elegans* (Decne.) Hemsl. Biol. Cent.-Amer., Bot. 2(12): 478. 1882. *Kohleria elegans* (Decne.) Loes., Bull. Herb. Boissier 7: 574. 1899. TIPO: Guatemala. "des régions montagneuses et tempérées du Guatimala" (tipo, tab. en página anterior a la 489 en Decne., 1849). [Dibujo hecho a partir de material cultivado proveniente de Guatemala]

Arbustos de 1–2 m de alto, plantas viloso-tomentosas, con tricomas hialinos frecuentemente rojizos. Hojas ligeramente anisófilas, lanceolado-elípticas, las grandes de 4–18 × 1.7–6.5 cm, las pequeñas de 4.9–8 × 2.4–4 cm, margen con 23 a 56 dientes, venas laterales 7 a 9; pecíolos 0.5–3.5 cm de largo, vilosos a pilosos, y en su base con una pequeña marca circular rojiza, y un pliegue que recorre el nudo de pecíolo a pecíolo; haz verde oscuro, liso; envés plano verde claro, domos estomatales bajos distribuidos de manera laxa, un estoma por domo; mesófilo en donde se distingue el parénquima esponjoso. Flores en cimas umbeladas de 4 flores; pedúnculos de 0.8–6 cm de largo; brácteas 6–13 × 0.5–3 mm, elípticas pecioladas, vilosas o pilosas; pedicelos 0.8–3.2 cm de largo, vilosos a pilosos, con tricomas como el tallo; cáliz con el tubo obcónico, 2–5 × 3–4 mm, hirsuto, lóbulos 0.6–7.5 mm × 0.8–3 mm, lanceolado subulados, verdes, vilosos a pilosos; corola tubular ligeramente ampliada hacia el limbo, ligeramente ventricosa, 2.5–3.5 cm de largo, 6–10 mm de largo en la garganta, 4–5 mm de ancho en la base, roja-anaranjada, pilosa por fuera, ± gruesa, no translucida, glabra por dentro, células epidérmicas de la superficie adaxial con las paredes anticlinales irregularmente poligonales y paredes periclinales lisas, lóbulos 2.5–4 × 3–4 mm, suborbiculares, ± expandidos, eroso-denticulados; filamentos 2.7–3.1 cm de largo, pilosos o casi glabros, anteras 1.5–1.7 × 1.5–1.7 mm, incluidas en la corola, estaminodio de 0.3–0.4 mm de largo; nectario de 3–5 mm de alto; ovario densamente piloso, estilo 1.2–2.9 cm, pilósulo con tricomas glandulares, incluido en el tubo de la corola. Cápsula de 7–9 × 4.5–7 mm, oblongo, venas no evidentes, pardo en material seco; semillas 0.3 mm, pardo-rojizas.

Ejemplares de esta especie se han localizado en México, por el momento, en el estado de Chiapas y en Guatemala. Se establece en bosque caducifolio, bosque mesófilo de montaña y bosque de *Pinus–Quercus*, a 850–2500 m. Florece de septiembre a abril (información disponible en los ejemplares de herbario revisados).

Moussonia elegans es distinta de otras especies descritas del género. Se caracteriza por el indumento generalmente viloso-tomentosas en casi toda la planta, frecuentemente con tricomas rojizos, cimas umbeladas más cortas que las hojas, con cuatro flores y dos brácteas foliosas evidentes; flores sobre pedúnculos cortos, cáliz hirsuto, con los lóbulos lanceolado-subulados, las corolas rojo-anaranjadas, ligeramente ventricosas, ampliadas hacia el limbo,

más o menos gruesas, no translúcidas, pilosas, con los lóbulos expandidos, eroso-denticulados, y los estambres y estigma incluidos.

Debido a la aparente semejanza en la forma y color de las corolas, algunas de las especies que se publicaron posteriormente a *Moussonia elegans*, fueron incluidas en ella por autores como Fritsch (1913), Morton (1967), Gibson (1974), Wiehler (1975a) y Kvist y Skog (1992), por lo que esta última llegó a tener una amplia sinonimia. Las especies y variedades que fueron incluidas en algún momento son: *M. formosa* Van Houtte ex Regel (Fritsch, 1913), *M. costaricensis* Klotzsch ex Oerst., *M. papillosa* Oerst. ex Hanst., *Isoloma jaliscanum*, *Kohleria papillosa* var. *sericea* Fritsch, *K. collina* Brandegee, *K. pedunculata* Brandegee, *K. papillosa* var. *pendula* y *K. papillosa* var. *solitaria* C. V. Morton.

Al comparar las características distintivas encontradas en el protólogo con las que presenta la especie en sentido amplio, era evidente que se trataba de un complejo. Era la única especie con amplia variación tanto morfológica como anatómica, lo cual, al pretender incluirla en una clave de determinación del género, quedaba ubicada en diferentes partes de la clave, ya que presentaba, por ejemplo, diferentes tipos de indumento, el haz podría ser liso (*Moussonia elegans* s. str.), densamente papilado (*M. jaliscana*) o laxamente papilado (*M. papillosa*), dicasios de 3 ó 4 flores o incluso flores solitarias (*Kohleria collina*), inflorescencias más cortas que las hojas (*K. collina*) o más largas (*K. pedunculata*), lóbulos del cáliz linear-lanceolados (*M. costaricensis*) u ovado-lanceolados (*K. papillosa* var. *pendula*) por ejemplo, corolas translúcidas (*M. papillosa* var. *solitaria*) o no (*M. papillosa*), ovario densamente piloso (*M. elegans* s. str.) o casi glabro (*K. pedunculata*), tubo del cáliz obcónico (*K. collina*) u obcónico-eliptico (*M. papillosa*), etc. Cada sitio de la clave en general, podía corresponder a alguna de las especies de la sinonimia. Además, el amplio rango de variación permitía que ejemplares que no podían ser ubicados en alguna otra especie fuera del complejo, fueran incluidos en ese concepto tan amplio que era *M. elegans*. Algunos de estos ejemplares ya han sido descritos recientemente como especies nuevas (Ramírez-Roa, 2007a, 2007b).

Nomenclatura

Se trató de localizar material original en el que se pudiera haber basado Decaisne para hacer la descripción de esta especie, pero hasta el momento no se ha encontrado (Roxana Yockteng [P], com. pers.). También, al comienzo del estudio del complejo, se pensó en la posibilidad de epitificar la especie (Art. 9.7, McNeill et al., 2006). Sin embargo, se considera que el dibujo y la descripción proporcionan las características suficientes para reconocer a la especie.

En este trabajo se presentan solamente las diferencias anatómicas y morfológicas que se encuentran en dos de las especies que formaban este complejo. Sin embargo, la decisión tomada aquí para considerar a *Moussonia elegans* en sentido estricto, se basa en las observaciones hechas tanto en los demás taxones que han formado el complejo según Wiehler (1975a), así como en las especies restantes del género. La segregación de las demás especies que han integrado el complejo y los cambios nomenclaturales pertinentes, será presentada en su momento en la revisión del género (Ramírez Roa, en preparación).

Ejemplares examinados. GUATEMALA. **Alta Verapaz:** near San José SE of Tactic, 1500 m, *Standley 69659* (F). **Baja Verapaz:** Mtn. side N of Divide N of Santa Rosa, 1650 m, *Standley 69878* (F). MÉXICO. **Chiapas:** above Finca Cuxtepec, *Breedlove 48663* (MEXU, MO); near municipal border betw. Bochil & Jitotol, 1300–1500 m, 18 Oct. 1963, *D. L. & M. L. Denham 62/463* (US).

4. Moussonia jaliscana (S. Watson) D. L. Denham ex Ramírez-Roa, comb. nov. Basiónimo: *Isoloma jaliscanum* S. Watson, Proc. Amer. Acad. Arts 25: 159. 1890. TIPO: México. Jalisco: sandy damp walls of gullies, near Guadalajara, Nov. 1888, *C. G. Pringle 1828* (holotipo, US-0086832!; duplicados, BM!, F!, NY!, US-01336337!).

Arbustos de 1–2 m de alto, plantas vilosa, con tricomas amarillentos. Hojas casi isofilas lanceolado-elípticas, las grandes de 4–18 × 1.7–6.5 cm, las pequeñas de 4.9–8 × 2.4–4 cm, margen con 23 a 56 dientes, venas laterales 7 a 9; pecíolos 0.5–3.5 cm de largo, vilosos; haz verde claro, generalmente densamente papilado en toda la superficie o hacia el margen, con la epidermis brillosa en algunas porciones, células epidérmicas alrededor de los tricomas de varias hileras, diferentes a las demás células adyacentes; envés sinuoso, verde-amarillento, domos bajos, distribuidos de manera ± densa, un estoma por domo; mesófilo diferenciado en parénquima esponjoso. Flores en cimas umbeladas de 4 flores, generalmente varias cimas hacia el ápice de la planta; pedúnculos de 0.8–6 cm de largo; brácteas 6–13 × 0.5–3 mm, lineares, vilosas; pedicelos gruesos, 0.8–3.2 cm de largo, vilosos, con tricomas amarillentos; cáliz con el tubo obcónico triangular, 2–5 ×

3–4 mm, cortamente viloso, lóbulos 0.6–7.5 × 0.8–3 mm de ancho, lanceolado-triangulares, verdes; corola tubular, ventricosa, constreñida por arriba de la base y de la garganta, 2.5–3.5 cm de largo, 6–10 mm de ancho en la garganta, 4–5 mm de ancho en la base, roja-anaranjada, cortamente vilosa, más o menos gruesa y no translucida, células epidérmicas de la superficie adaxial con paredes anticlinales de forma irregular poligonal y periclinales con pequeñas papilas arregladas de manera densa, lóbulos 2.5–4 × 3–4 mm de ancho, oblongos, más o menos expandidos, crenados; filamentos 2.7–3.1 cm, pilosos o casi glabros, anteras 1.5–1.7 × 1.5–1.7 mm, incluidas en la corola, estaminodio de 0.3–0.4 mm de largo; nectario de 3–5 mm de alto; ovario densamente piloso, estilo 1.2–2.9 cm de largo, pilósulo con tricomas glandulares, incluido en el tubo de la corola. Cápsula de 7–9 × 4.5–7 mm, oblonga, venas no evidentes, parda en material seco; semillas 0.3 mm, pardo-rojizas.

Especie endémica de México, presente en Colima y Jalisco. Se establece en bosque húmedo de montaña, bosque mesófilo de montaña, bosque de *Pinus–Quercus*, a 1350–2220 m. Florece de julio a enero, fructifica en abril y octubre (información obtenida de los ejemplares de herbario revisados).

Moussonia jaliscana se distingue por la pubescencia vilosa principalmente de los tallos, el haz papiloso, por la presencia de tricomas con la base multicelular, ya sea en toda su superficie o hacia el margen del haz, la epidermis generalmente lustrosa, el envés sinuoso, varias cimas de cuatro flores hacia el ápice de la planta, el cáliz obcónico y cortamente viloso, los lóbulos lanceolado-triangulares de longitud variable, la corola ventricosa, con la garganta constreñida y cubierta de manera característica por pubescencia villoso-canescente, además de un fruto oblongo.

La especie que más se parece a *Moussonia jaliscana* es otro de los sinónimos de *M. elegans* s.l., *M. papillosa*, la cual se distingue fácilmente por la pubescencia pilosa-canescente en buena parte de la planta, el haz reticulado-rugoso dando una apariencia laxamente papilosa a la superficie, la epidermis opaca, el envés con hundimientos los cuales corresponden a la superficie rugosa del haz, cáliz obcónico-elíptico y densa y largamente viloso-canescente, lóbulos largamente lanceolado-elípticos, con un fruto largamente oblongo-elíptico. *Moussonia jaliscana* se distribuye en Puebla y Veracruz. Debido a las características particulares que presenta *M. papillosa* con respecto a *M. jaliscana* y *M. elegans*, además de las diferencias en la distribución geográfica, se le está considerando nuevamente como una especie distinta (Ramírez-Roa y Skog, datos no publicados), tal como lo hicieron en su momento Hanstein (1865), Fritsch (1913) y Morton (1967).

Nomenclatura

Watson indicó en el protólogo de esta especie dos ejemplares distintos como respaldo del nombre, siendo el primero *Pringle 1828* (US) y el segundo *Palmer 577*. El material de herbario perteneciente a estas dos colectas, depositados en diferentes herbarios, tienen indicado que son sintipos o isosintipos. Sin embargo, en el protólogo, al terminar la descripción de la especie y asignar el ejemplar tipo, Watson (1890: 159) indicó: "On the Rio Blanco, Jalisco; 1888 (n. 1828); also collected by Dr. Palmer in 1886 (n. 577)." Considerando la redacción de este párrafo, el material de herbario de G. C. Pringle con número 1828 es el holotipo. El párrafo "...; also collected by ..." nos indica que Watson además observó otra colecta, por lo que el material de E. Palmer con número 577 es adicional, y debemos considerarlo como paratipo indicado en el protólogo. Con respecto al material tipo *G. C. Pringle 1828* depositado en el herbario US, existen dos ejemplares, uno de los cuales tiene el número de registro 0086832 y código de barras 00317640 y el otro tiene el número 01336337, con los tres primeros números corregidos a mano y código 00126597. Consideramos que el ejemplar con el número de registro 0086832, por ser mucho más antiguo en la colección y no tener enmiendas, debe ser considerado el que designó Watson como holotipo, y probablemente era el único material disponible en ese momento. El material restante de *G. C. Pringle 1828* y *E. Palmer 577* pudo haber ingresado a la colección tiempo después.

Isoloma jaliscanum, referida ahora como *Moussonia jaliscana*, fue primeramente incluida en la sinonimia de *Kohleria papillosa* [≡ *M. papillosa*] por Fritsch (1913). Posteriormente Morton (1967) la incluye en la sinonimia de *K. papillosa*. Y, por último, Wiehler (1975a) y Kvist y Skog (1992) la consideraron sinónimo de *M. elegans*. Con respecto a *M. papillosa* ya se han indicado las diferencias. Las diferencias de *M. elegans* son el indumento generalmente viloso-tomentosas en casi toda la planta, frecuentemente con tricomas rojizos, con los lóbulos lanceolado-subulados, las corolas rojo-anaranjadas, ligeramente ventricosas, ampliadas hacia el limbo y pilosas.

En cuanto al cambio del nombre de la especie de *Isoloma* a *Moussonia*, el ejemplar *Pringle 11072* (MEXU) tiene indicado en la etiqueta de determi-

nación que realizó D. L. Denham en 1971 con el cambio de género, incicando además, adelante del nombre "in Schad". Sin embargo, nunca publicó el cambio. Por este motivo se le está dando el crédito en la nueva combinación.

Ejemplares examinados. MÉXICO. **Colima:** Rancho el Jabalí, ca. 20 km N de Colima, *Rico y Martínez 942* (MEXU, US). **Jalisco:** near Guadalajara, *Pringle 11072* (MEXU, NY, US); *Pringle 11660* (LL).

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Cover illustration. *Emmotum yapacanum* R. A. Howard, drawn by Bruno Manara.

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THE FERN GENUS *POLYSTICHUM* (DRYOPTERIDACEAE) IN COSTA RICA[1]

David S. Barrington[2]

Abstract

The fern genus *Polystichum* Roth (Dryopteridaceae) remains one of the most difficult genera taxonomically. In this work, I provide an identification guide to the Costa Rican *Polystichum* species in the context of an evaluation of characters and evolution in the genus in the Neotropics. Key characters are those of petiole and pinna-rachis scales, ultimate segment shape, and indusium. There are 12 species in the country, of which three are allopolyploids (*P. lilianiae* Barrington, *P. orbiculatum* (Desv.) J. Rémy & Fée, and *P. talamancanum* Barrington). The species' distributions vary: while five are widespread in Tropical America, two are at the southern end of their range (*P. alfaroi* (Christ) Barrington and *P. speciosissimum* (A. Braun ex Kunze) R. M. Tryon & A. F. Tryon), and two are at the northern end (*P. dubium* (H. Karst.) Diels and *P. nudicaule* Rosenst.). Three are confined to Costa Rica and Panama: *P. concinnum* Lellinger ex Barrington and the allopolyploids *P. lilianiae* and *P. talamancanum*. Essentially a denizen of wetter montane regions throughout the world, the genus in Costa Rica is most prominent in higher-elevation rainforests and to a lesser extent in the páramos of the Cerro de Talamanca. The names *P. aculeatum* var. *flavidum* Rosenst., *P. nudicaule* Rosenst., and *P. opacum* Rosenst. are lectotypified.

Resumen

Polystichum Roth (Dryopteridaceae) es un género de helechos con dificultades taxonómicas que complican la identificación de sus especies. En este trabajo, presento una clave de identificación taxonómica para las especies de *Polystichum* en Costa Rica analizando diferente caracteres morfológicos y la evolución del género en el Neotrópico. Los caracteres más importantes pertenecen a las escamas de peciolo y raquis de la pinna, forma de los últimos segmentos, e indusio. En el país se encuentran 12 especies, incluyendo tres poliploides. La distribución de las especies es variable: cinco se ubican en toda la America tropical, dos se extienden en el borde sur y dos en el borde norte de estas áreas tropicales, y tres (incluyendo dos allopoliploides) se limitan a Costa Rica y Panamá. *Polystichum* es un componente común de las selvas mas húmedas de montañas en todo el mundo, en Costa Rica el género se encuentra típicamente en elevaciones altas, en selvas lluviosas y en páramos del Cerro de Talamanca. Los nombres *P. aculeatum* var. *flavidum* Rosenst., *P. nudicaule* Rosenst, y *P. opacum* Rosenst. son lectotipificados.

Key words: Costa Rica, Dryopteridaceae, ferns, *Polystichum*.

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Among the prominent ferns in the high-montane forests and páramos of Costa Rica are species of the terrestrial fern genus *Polystichum* Roth, known in English as "holly ferns." *Polystichum*, one of the 10 largest fern genera (data from Smith et al. [2006]), is most diverse in subtropical regions of both the New World and Old World, but it is also diverse in tropical montane regions. In addition, the genus can be found in the alpine zone—in the Sino-Himalayan Region (sensu Takhtajan, 1986), in New Guinea, and in the Neotropics. About one third of the species in the genus is found in the American tropics, where there are three centers of diversity: the Greater Antilles (31 species [Mickel, 1997]), Mexico and Guatemala (18 species [Stolze, 1981; Mickel & Smith, 2004]), and the North and Central Andes (29 species [Kessler et al., 2005; McHenry & Barrington, unpublished]).

The taxonomy of the genus *Polystichum* remains unresolved in spite of substantial recent study (Roux, 2000; Little & Barrington, 2003; Driscoll & Barrington, 2007; Lu et al., 2007; Li et al., 2008). It is possible to delineate a monophyletic genus *Polystichum* as long as *Cyrtomium* C. Presl s. str. is excluded; the species allied to *C. balansae* (Christ) C. Chr. are polystichums (Li et al., 2008). However, the subgeneric taxonomy is in chaos because (1) the key works on sections, by Daigobo (1972) and Roux (2000), are not based on a critical review of world morphology or genetic variation; (2) sections have been typified by allopolyploids (e.g., *Polystichum* sect. *Aculeata* Christ and *Polystichum* sect. *Lasiopolystichum* Daigobo); and (3) morphological convergence is rampant in the genus. In fact, given our present primitive understanding of phylogeny and character variation in the genus, it would be folly to attempt a subgeneric classification.

Costa Rica lies in a unique geographic position in the American tropics, between the high-montane regions of Mexico and Guatemala to the northwest and the northern Andes to the east and south. The provenance of the higher-elevation fern diversity in Costa Rica is a mix of species with two geographic patterns: species also found in the Andes and species that are common to the north in southern Mexico and Guatemala (Barrington, 2005). There is a tendency in the Costa Rican ferns for the páramo species to extend to the south and the montane-forest species to extend to the north (Barrington, 2005). *Polystichum* in Costa Rica fits these general patterns, but with some notable exceptions.

Neotropical *Polystichum* is monophyletic, based on a molecular phylogenetic analysis of a sample of nine species included in a recent world phylogeny (Driscoll & Barrington, 2007). In this analysis, the polystichums found in Costa Rica fall into three groups. *Polystichum speciosissimum* (A. Braun ex Kunze) R. M. Tryon & A. F. Tryon is sister to all the other species. The remaining species fall into two monophyletic lineages. The first is an indusiate alliance (which I call the Mayan clade) including species endemic to Central America. The second is an exindusiate lineage (the Andean clade) including species endemic to the Central Andes.

Identification of *Polystichum* species in the field and in the herbarium remains an extraordinary challenge, and herbaria continue to have high levels of misidentification in the genus. Forty years of fieldwork in Costa Rica have yielded a diversity of insights into the delimitation, habitat preference, and geographic provenance of the species in the country. In this paper, I seek to synthesize these data into a treatment of the Costa Rican species that will (1) serve as an identification guide, (2) provide insights into the natural history and evolutionary biology of these elegant and confusing plants, and (3) point the way to addressing the remaining problems.

Materials and Methods

Herbarium materials from A, AAU, BM, CR, DS, E, GH, K, L, MO, NA, NY, P, UC, US, and VT formed the basis for this study. The materials at VT (for which there are often duplicates at CR) are the result of 21 excursions to Costa Rica between 1970 and 2011. I have made numerous observations in the field in Costa Rica that provide insight into the diversity and ecology of Costa Rican *Polystichum* species. An array of genetic analyses of Costa Rican polystichums from my lab (e.g., Barrington, 1990, 2003; Little & Barrington, 2003; Driscoll & Barrington, 2007) informs the morphological work reported here.

General Considerations

The Nature of Variation in Costa Rican *Polystichum*

Four kinds of problems complicate the naming of *Polystichum* species: (1) phenotypic variation, (2) changes associated with increased size over an individual's lifespan, (3) challenges presented by indument characters, and (4) hybridization. However, paucity of characters that are stable within species and labile between species is not a problem. There is a wealth of morphological characters to choose from (Little & Barrington, 2003), and close analysis yields characters with real power to distinguish even closely allied species (e.g., Barrington, 2003).

Phenotypic variation is rampant: characters such as petiole length, petiole color, and the curvature of pinnule margins are all labile in relation to variation in light levels. For instance, plants from the highly insolated habitats above treeline in the Cerro de la Muerte have much shorter petioles and much more recurved segments than genetically identical plants from the small shaded stream banks nearby. Unfortunately, these characters are prominent and have often been used as the basis for describing species in *Polystichum*.

Variation with size is also common. For instance, though valuable in distinguishing species, petiole scale color varies with size of leaf and thus presumably with age of the individual among fertile plants of *Polystichum*. The key variable is value in the sense of the Munsell color solid (e.g., Munsell, 1966); larger, older plants have darker scales than younger, smaller plants of the same species. Shape also varies with size: it is common for small fertile leaves of a species to differ in shape from larger leaves, especially in overall length:width ratio and in the length of the basal pinnae. Leaf dissection presents similar patterns: some species—notably *P. alfaroi* (Christ) Barrington, *P. hartwegii* (Klotzsch) Hieron., and *P. platyphyllum* (Willd.) C. Presl—are prone to increase in lamina dissection with increase in plant size.

Though critical to species identification in *Polystichum*, indument presents several challenging problems; most important is positional equivalence. An indument character must be scored from the same position on the same organ across the plants of the study set to ensure the homology inherent in the character. For instance, although the shape of pinnarachis scales is one of the most powerful characters for distinguishing *Polystichum* species, the variation in scales lying in different positions on the pinnarachis (base of the pinnules vs. between the pinnule attachments) can obscure the stable character states that divide species. Petiole scales present another problem of position. Since the scales at the base of the petiole are routinely different from those above the base, distinguishing the basalmost scales from the more distal is critical. However, collections with leaves but no stems often do not have the material to ensure that the most proximal portion of the petiole was collected. To make matters worse, some of the most useful indument characters in *Polystichum* are vulnerable to loss in herbaria. Notable are the features of the cilia on the edges of petiole scales, which are powerful characters for distinguishing species. The more delicate cilia are especially vulnerable to being worn off during collection or routine handling of herbarium specimens, making the characters unscorable.

Hybridization and polyploidy are common in Costa Rican *Polystichum* (Barrington, 1990, 2003). Three Costa Rican polystichums are allopolyploids, and four hybrids have been documented. Emblematic of the problems presented by hybrids in Costa Rica is the backcross hybrid between *P. talamancanum* Barrington and *P. concinnum* Lellinger ex Barrington, which is common in mixed populations with its tetraploid parent in disturbed terrain above treeline in the Cerro de la Muerte. The morphological discontinuity between the two progenitors is largely obscured by the backcross hybrid.

DIVERSITY, ECOLOGY, AND BIOGEOGRAPHY

The genus *Polystichum* in Costa Rica comprises 12 species; nine of the 12 are diploid. Ecologically, two of the nine diploids (*P. nudicaule* Rosent. and *P. speciosissimum*) are characteristic páramo species growing above 3000 m. Five other diploid species are found in forests. These include two montane rainforest species (forest classification follows Holdridge [1987] throughout), one of which has among the largest leaves in the genus (*P. concinnum*), while the other is a diminutive species with unusually thin rhizomes for the genus (*P. turrialbae* Christ). The remaining three are to be found in premontane moist to wet forests (*P. alfaroi*, *P. muricatum* (L.) Fée, and *P. hartwegii*). Finally, two diploids (*P. platyphyllum* and *P. dubium* (H. Karst.) Diels) are characteristic of stream banks and earthen banks in premontane wet and rainforests in Costa Rica. The diploids from the forests are indusiate; those from páramo and stream bank are exindusiate. Biogeographically, the forest diploids are related to indusiate species endemic to Mexico and Central America, whereas most of the páramo and stream bank species are related to exindusiate species confined to the Andes. The single exception is *P. speciosissimum*, a páramo species disjunct from Mexico and Guatemala. Among the diploids, only the montane rainforest *P. concinnum* is endemic to the Talamanca massif; all others are either more widely distributed to the north (*P. alfaroi*, *P. speciosissimum*) or to the south (*P. dubium*, *P. nudicaule*) or are broadly distributed in the American tropics (*P. hartwegii*, *P. muricatum*, *P. platyphyllum*, *P. turrialbae*).

The three remaining species in Costa Rica are allotetraploids, all from high-montane forests and páramos. Two are endemic: *Polystichum lilianiae* Barrington (high-montane) combines the heritage of the widespread *P. turrialbae* with an unknown second species, whereas *P. talamancanum* (páramo) com-

bines the heritage of the endemic *P. concinnum* with an unknown second progenitor. The remaining tetraploid is *P. orbiculatum* (Desv.) J. Rémy & Fée (páramo). A prominent member of the central and northern Andean páramo communities (Barrington et al., 1986), *P. orbiculatum* is found north of Costa Rica only on Volcán Tacaná at the border between Mexico and Guatemala (Smith, 1981). *Polystichum orbiculatum* does not yet have identified living progenitors, but one of its progenitors is also the unknown second progenitor of *P. talamancanum* (Barrington, 1990). Small spores encountered in northern Andes individuals suggest that an undetected diploid progenitor may be there (Barrington et al., 1986).

Polystichum is largely a montane genus throughout the world. In Costa Rica the genus is only found in the mountains. It becomes ecologically prominent at upper elevations on the Cordillera de Talamanca and the Cordillera Central (the volcanoes). Few records exist from the Cordillera de Tilarán and the Cordillera de Guanacaste. The small mountain ranges in the Central Valley (the Cerro de la Carpintera southwest of Cartago and the Cerros de Escazú south of San José) also host polystichums, and there are historical (lost) stations in the Central Valley itself, especially along the rivers. Three species of Costa Rican polystichums are of conservation concern; all are from lower montane and premontane forests under substantial development pressure. *Polystichum dubium*, for which a single Costa Rican station is known to be extant, appears to be most critical. Also of concern are *P. platyphyllum* and *P. hartwegii*, both of which are represented by few modern collections from the country.

Taxonomic Treatment

Polystichum Roth, Tent. Fl. Germ. 3(1): 31, 69. 1799, nom. cons. TYPE: *Polystichum lonchitis* (L.) Roth, Tent. Fl. Germ. 3(1): 31, 69. June–Sep. 1799.

Plants terrestrial; rhizomes erect or ascending, rarely branched; indument entirely of scales including uniseriate scales (sensu Moran, 1987). Leaves of fertile individuals monomorphic, clustered at the stem apex; petioles adaxially sulcate, with more than 2 leaf traces, edges of the petiole scales usually with cilia (except *Polystichum muricatum*) but without a histologically differentiated margin (except *P. alfaroi*); blades usually 2-pinnate (rarely 1-pinnate or 2-pinnate pinnatisect), gradually reduced at the apex (not conform or subconform); ultimate segments spinulose or at least dentate-mucronate; veins free and forked (occasionally anastomosing without included veinlets in *P. dubium*), extending to the margin, lacking hydathodes; sori round, abaxial or terminal on the veins; indusiate or not, the indusia true (abaxial on the receptacle) and peltate or false (a modified segment edge, only in *P. speciosissimum*).

Taxonomic Key to the Species of Costa Rican *Polystichum*

1a. Blades once-pinnate (indusia absent) ... 3. *P. dubium*
1b. Blades twice-pinnate to twice-pinnate pinnatisect 2
2a. Indusia absent (but present in a few sori on some individuals of *P. talamancanum*) 3
3a. Bulbil present at base of pinna near leaf apex, pinnules flat, below 2000 m ..... 9. *P. platyphyllum*
3b. Bulbil absent, pinnules strongly recurved except in deep shade, above 2800 m 4
4a. Pinnules deeply pinnatisect throughout, basal petiole scales orange ..... 10. *P. speciosissimum*
4b. Pinnules crenate (sometimes basally pinnatisect in *P. orbiculatum*), basal petiole scales various colors, but not orange 5
5a. Basal petiole scales atropurpureous or fuscous; pinnae, if ascendant, more than 6 times as long as wide 6
6a. Pinnae attenuate, the basal pinnae as long as or longer than the next distal, pinnules oblique to the pinna-rachis ..... 7. *P. nudicaule*
6b. Pinnae acuminate, pinnules attached at right angles to the pinna-rachis .... 11. *P. talamancanum*
5b. Basal petiole scales rufous; pinnae both ascendant and up to 6 times as long as wide ..... 8. *P. orbiculatum*
2b. Indusia present 7
7a. Small plants (leaves to ca. 50 cm) with small (up to 1 cm), stramineous basal petiole scales (fulvous to fuscous central stripe present in *P. lilianiae*), abundant very short cilia on the petiole scales, and broad-based pinna-rachis scales 8
8a. Pinnae acuminate; basal pinnae not the longest; pinnules of medial pinnae attached at right angles to pinna-rachis; petiole-base scales uniformly pale or with a weakly defined brown stripe at the center ..... 12. *P. turrialbae*
8b. Pinnae attenuate; basal pinnae the longest; pinnules of medial pinnae attached at about a 60° angle to pinna-rachis; petiole-base scales with a sharply defined brown stripe at the center ..... 5. *P. lilianiae*
7b. Medium to large plants (leaves 50 cm or more) with larger (1 cm or more), fuscous to rufous basal petiole scales (*P. muricatum* and *P. hartwegii* may have fuscous basal petiole scales with a narrow fulvous edge); petiole-scale cilia various but not abundant and short; pinna-rachis scales various.
9a. Indusia small (ca. 0.3 mm diam.), petiole-scale cilia absent ..... 6. *P. muricatum*
9b. Indusia ca. 0.5 mm to over 1 mm diam., petiole-scale cilia present 10
10a. Indusia over 1 mm diam.; pinnae ca. 3 cm wide; pinna-rachis scales filiform ..... 4. *P. hartwegii*
10b. Indusia 0.5–0.8 mm diam.; pinnae 1.5–2 cm wide; pinna-rachis scales various ..... 11.

11a. Pinna-rachis scales lanceolate; basal petiole scales narrow (ca. 6:1), conform; basal acroscopic pinnules of medial pinnae often shorter than the next distal pinnule ..... 2. *P. concinnum*
11b. Pinna-rachis scales filiform; basal petiole scales broad (ca. 4:1), marginate; basal acroscopic pinnules of medial pinnae longer than the next distal pinnule ..... 1. *P. alfaroi*

1. Polystichum alfaroi (Christ) Barrington, Rhodora 94: 328. 1992. Basionym: *Polystichum aculeatum* var. *alfaroi* Christ, Bull. Herb. Boissier, sér. 2, 4: 963. 1904. TYPE: Costa Rica. San José: Alajuelito, 1300 m, Mar. 1902, *A. Alfaro 16471* (holotype, P not seen; isotype, US!). Figure 2.

Polystichum aculeatum var. *flavidum* Rosenst., Repert. Sp. Nov. Regni Veg. 22: 9. 1925. TYPE: Costa Rica. Cartago: Cartago, 1400 m, *A. C. Brade 555* (lectotype, designated here, B not seen; isolectotype, UC-405822!).

Rhizome erect, reaching ca. 5 cm diam. Fronds typically 60–80 cm, spreading; petiole scales ca. 1.5 cm, lanceolate, marginate, rufous, petiole-scale cilia short and delicate. Laminae 2 to 3 times as long as wide, acuminate, 2-pinnate and crenate to 2-pinnate pinnatisect, without a bulbil; pinnae attenuate, ca. 8 times as long as wide, attached at right angles to the rachis, the basal pinnae often the longest; pinna-rachis scales filiform (or narrow-lanceolate), rufous; pinnules flat, obliquely attached throughout, the auricle weakly developed, the apex acute, spinules weak (developed only at apex and auricle), the basal acroscopic pinnule of the medial pinnae longer than the adjacent pinnule. Indusia ca. 0.6 mm in diam.

Discussion. *Polystichum alfaroi* is a large fern with notably lustrous upper leaf surfaces; the long pinnules with acute tips help to identify the species. The marginate petiole scales are unique among Costa Rican polystichums. The species honors Anastasio Alfaro (1865–1961), one of the prominent naturalists of the active scientific community in San José in the late 19th and early 20th centuries and long director of the Museo Nacional de Costa Rica.

Polystichum alfaroi occurs from 1100 to 2200 m on the Cordillera de Guanacaste, Cordillera Central, Cerros de la Carpintera, and the Cordillera de Talamanca including the Cerros de Escazú, mostly on leeward (southwest-facing) slopes. This distribution is apparently driven by *P. alfaroi*'s unique habitat among Costa Rican polystichums, the moist premontane forest, where it is a prominent fern (Barrington, 1992). This vegetation zone has been extensively cleared for agriculture, so the species is hard to find. The problem is epitomized by the type locality, now lost to urbanization in the Valle Central.

Geographically, *Polystichum alfaroi* presents a striking disjunct distribution, with the other populations in southernmost Mexico (Chiapas), Guatemala, and El Salvador (Barrington, 1992). *Polystichum alfaroi* is diploid, based on isozyme banding pattern (Barrington, 1992). It lies in the Mayan clade, based on molecular phylogenetic work (Driscoll & Barrington, 2007).

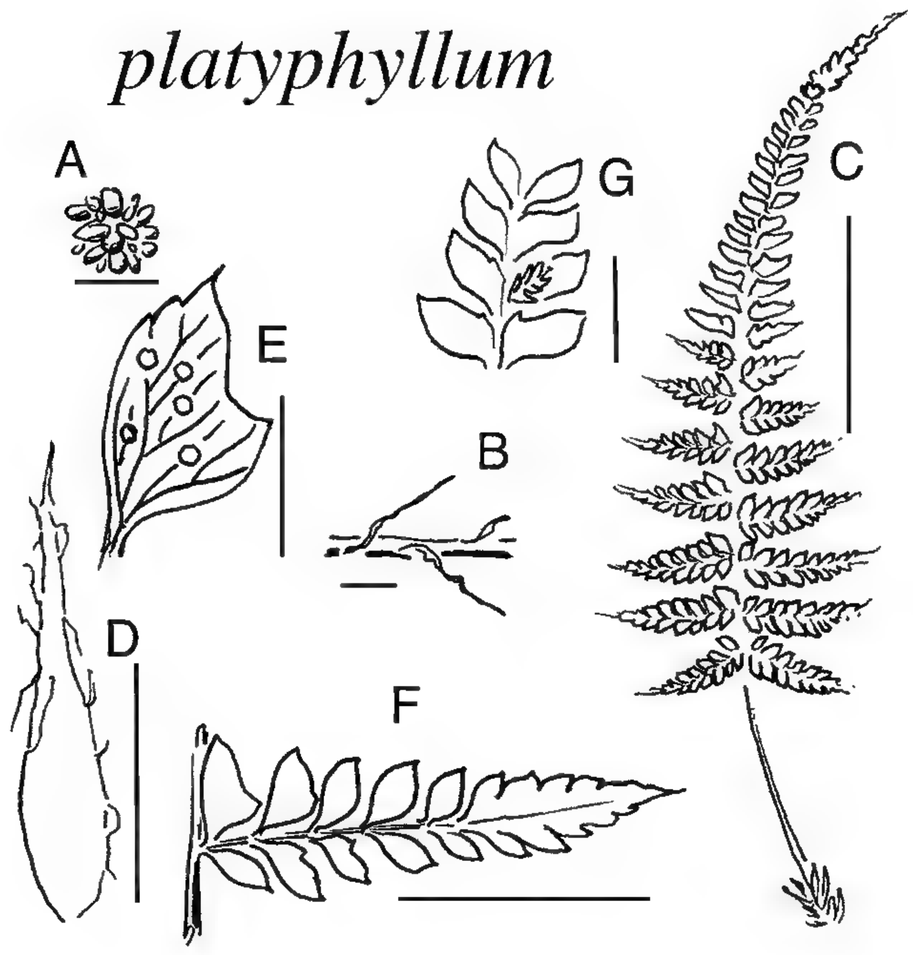
Remaining syntype material includes two collections from the Cerros de la Carpintera (*A. C. Brade 26*, *Brade 26a*).

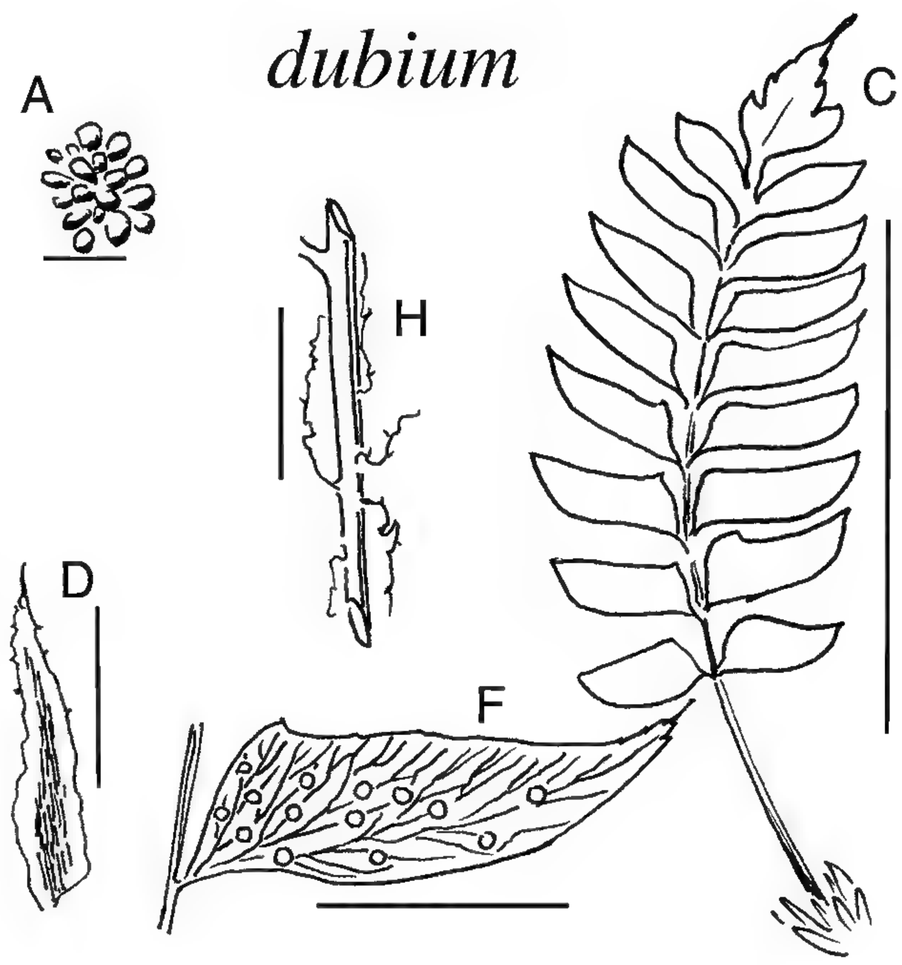
Selected specimens examined. COSTA RICA. **Cartago:** mtns. above Tres Ríos, *E. Scamman 7945* (GH). **Guanacaste:** Monteverde, Bajo del Tigre Reserve, *D. S. Barrington 2354* (VT). **San José:** La Carpintera, *R. Torres R. 170* (CR); Río Tiribi, Hda. La Verbena Alajuelita, *O. Jiménez L. 395* (CR, US).

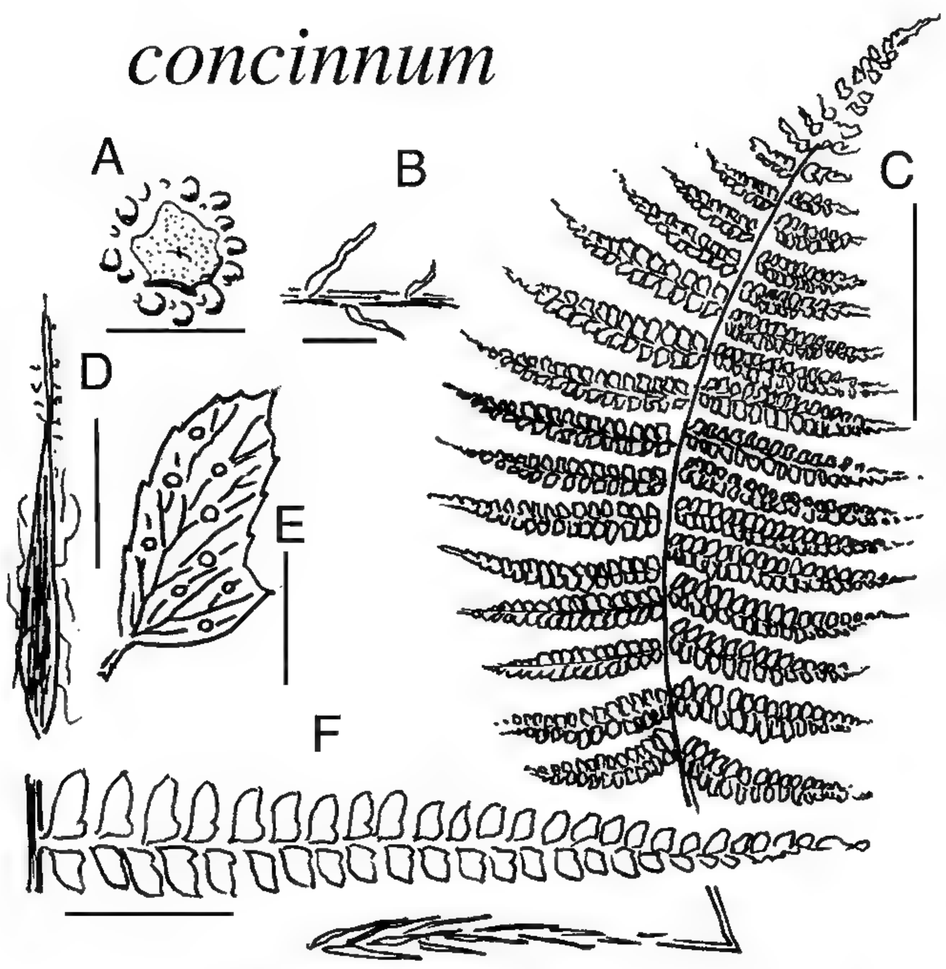
2. Polystichum concinnum Lellinger ex Barrington, Ann. Missouri Bot. Gard. 76: 367, fig. 1. 1989. TYPE: Costa Rica. San José: Villa Mills S of the Pan American Hwy. ca. 1 km E of Hotel La Georgina, ca. 3100 m, *D. S. Barrington 694* (holotype, GH!; isotype, VT!). Figure 1.

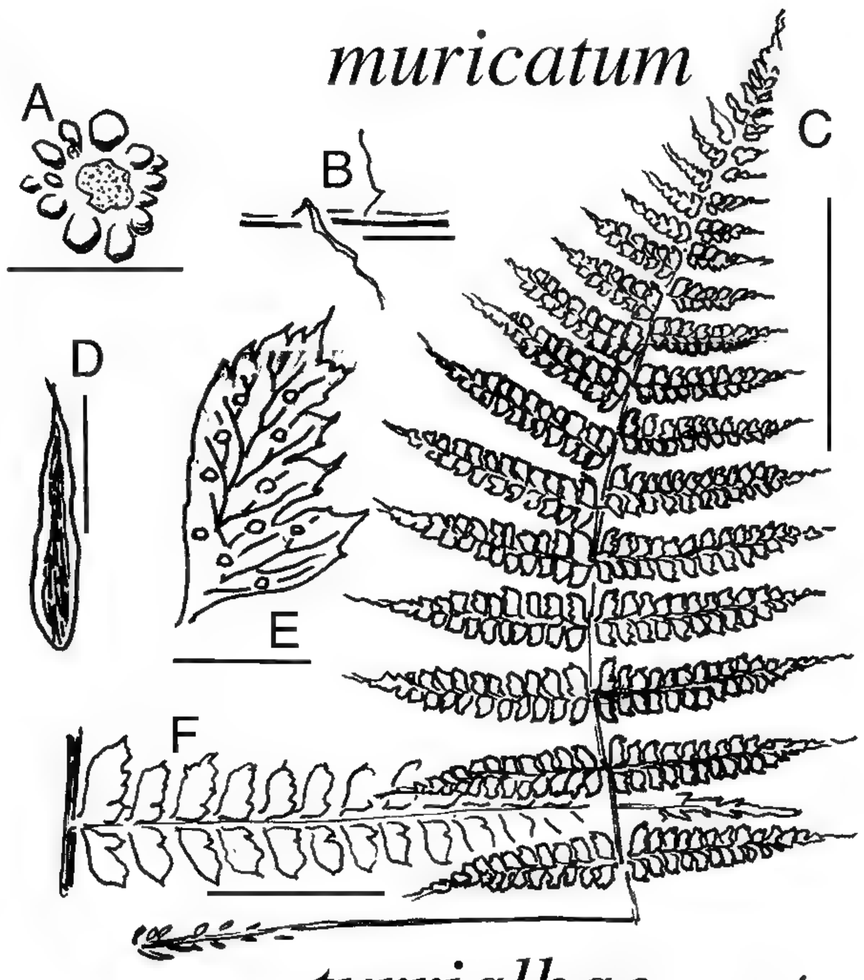
Rhizome erect, ca. 28 cm diam. Fronds to at least 1.2 m, spreading; petiole scales ca. 3 cm, narrow-lanceolate, conform, fuscous, petiole-scale cilia long and delicate below, short and stiff above. Laminae ca. 4 times as long as wide, acuminate, 2-pinnate and crenate, without a bulbil; pinnae attenuate, ca. 8 times as long as wide, attached at right angles to the rachis, the basal pinnae shorter than the next distal; pinna-rachis scales lanceolate, fulvous; pinnules flat, attached at right angles throughout, the auricle weakly developed, the apex acute, spinules weak (developed only at apex and auricle), the basal acroscopic pinnule of the medial pinnae often shorter than the adjacent pinnule. Indusia ca. 0.6 mm in diam.

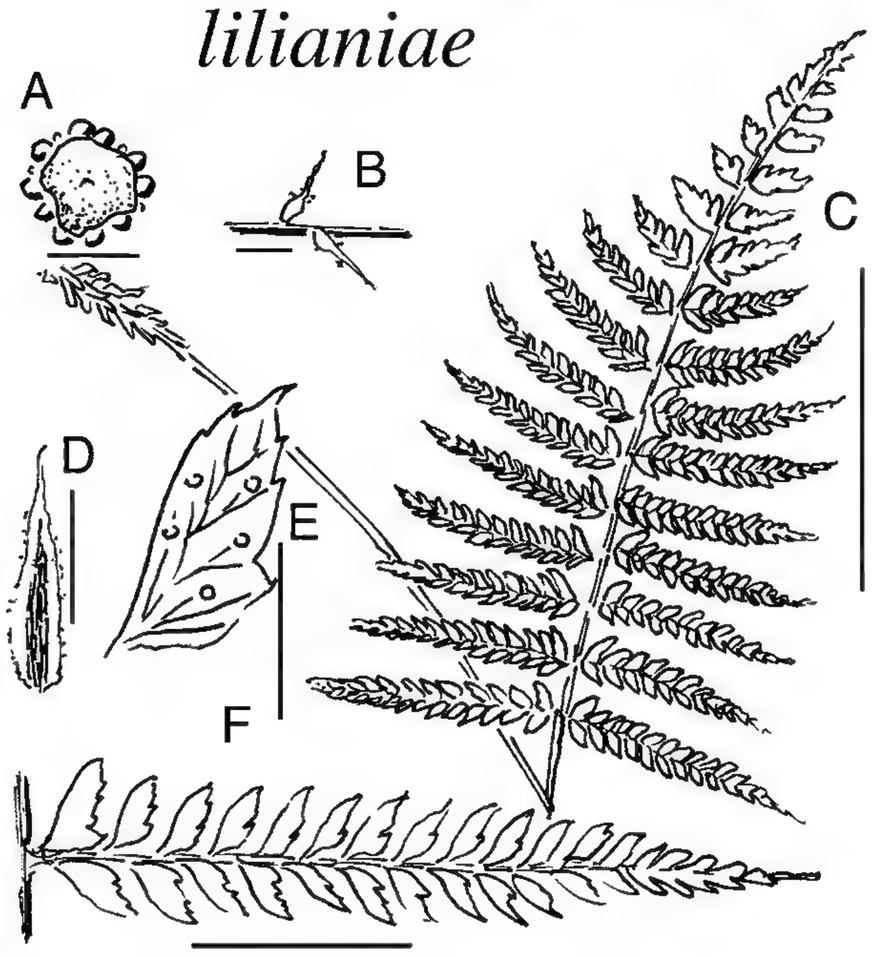
Discussion. *Polystichum concinnum* is the largest of the Costa Rican polystichums. The very dark, narrow-lanceolate petiole scales are shared only with the ordinarily exindusiate *P. talamancanum*. The species is unique among Costa Rica polystichums in often having the basal pinnules of the pinnae shorter than the rest. Young mature individuals from open sites, such as road cuts along the Pan American Highway, are superficially quite different from the large old-forest plants of this species; the lamina is broader, the pinnules are entire, and the lamina color is more yellow-green. These plants are not genetically distinct in their isozyme profiles (Barrington, unpublished). Where *P. concinnum* grows near highways, it commonly has sori transformed into globose galls up to 8 mm in diameter that bear untransformed











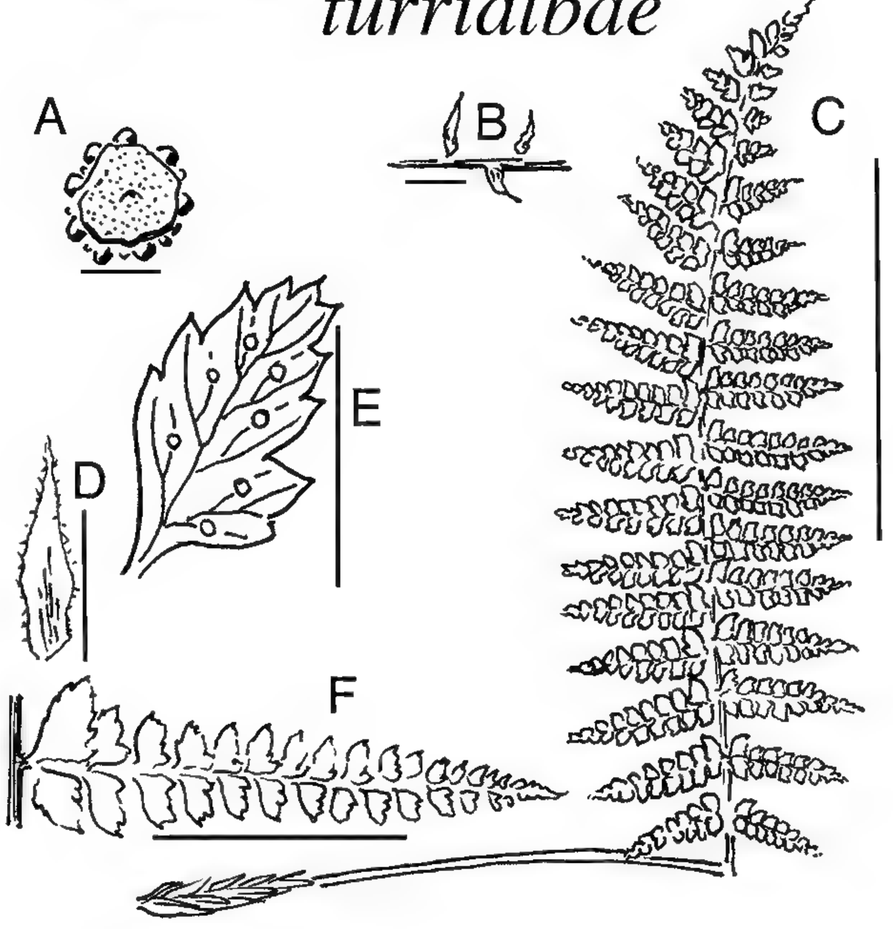
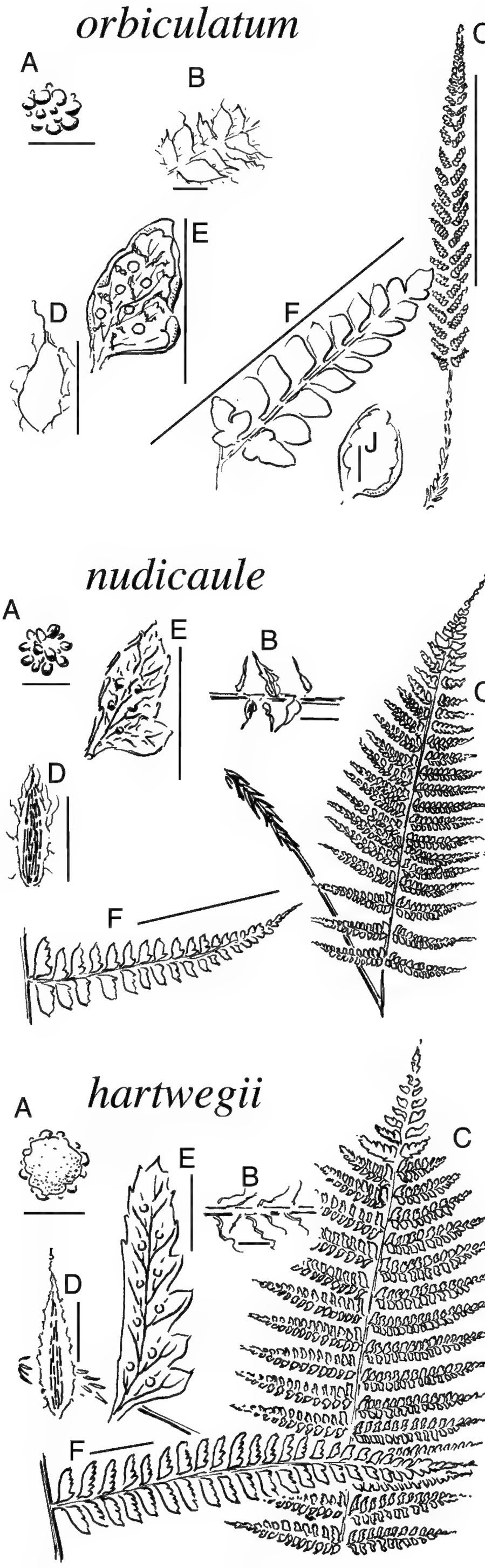
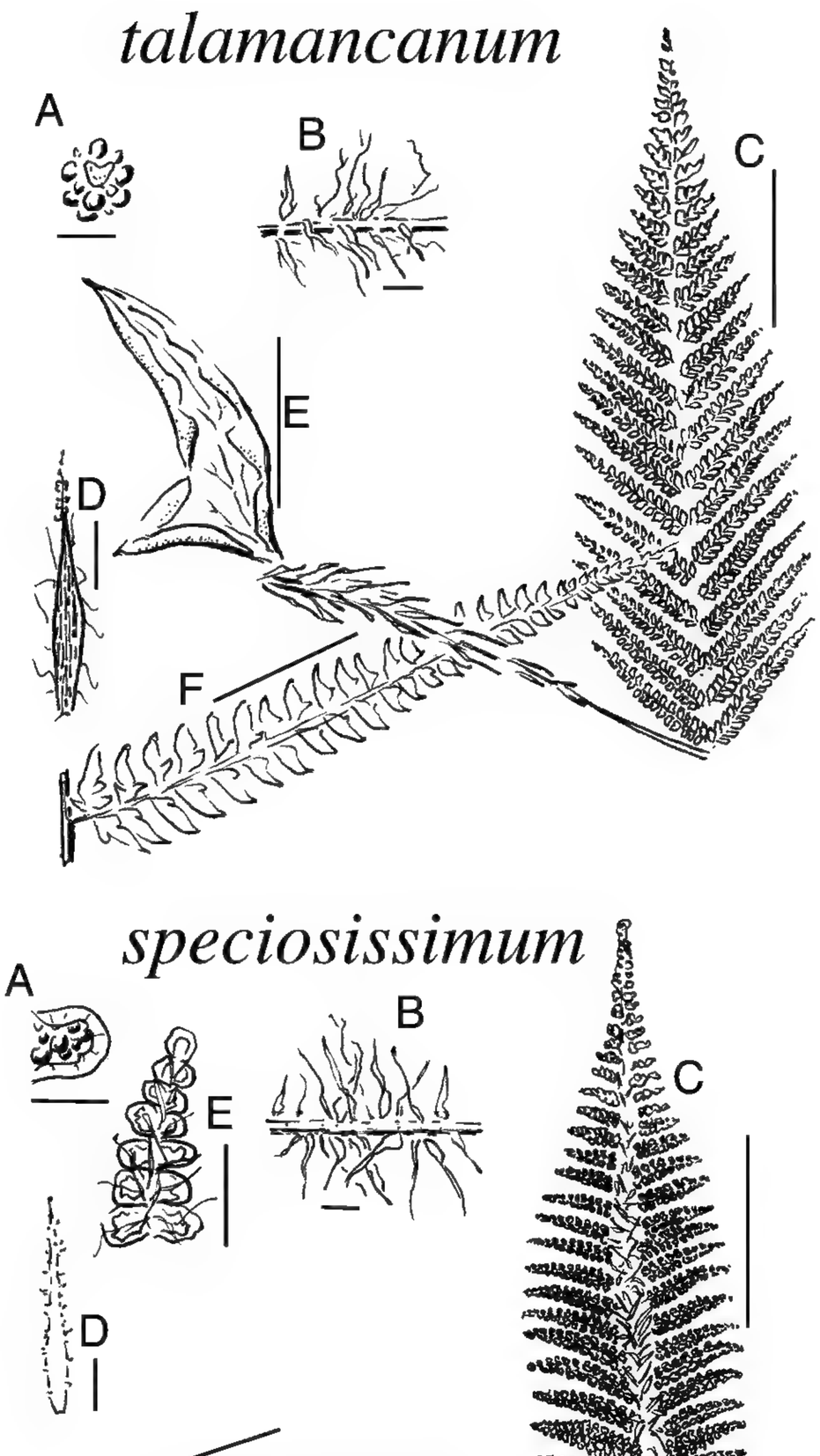
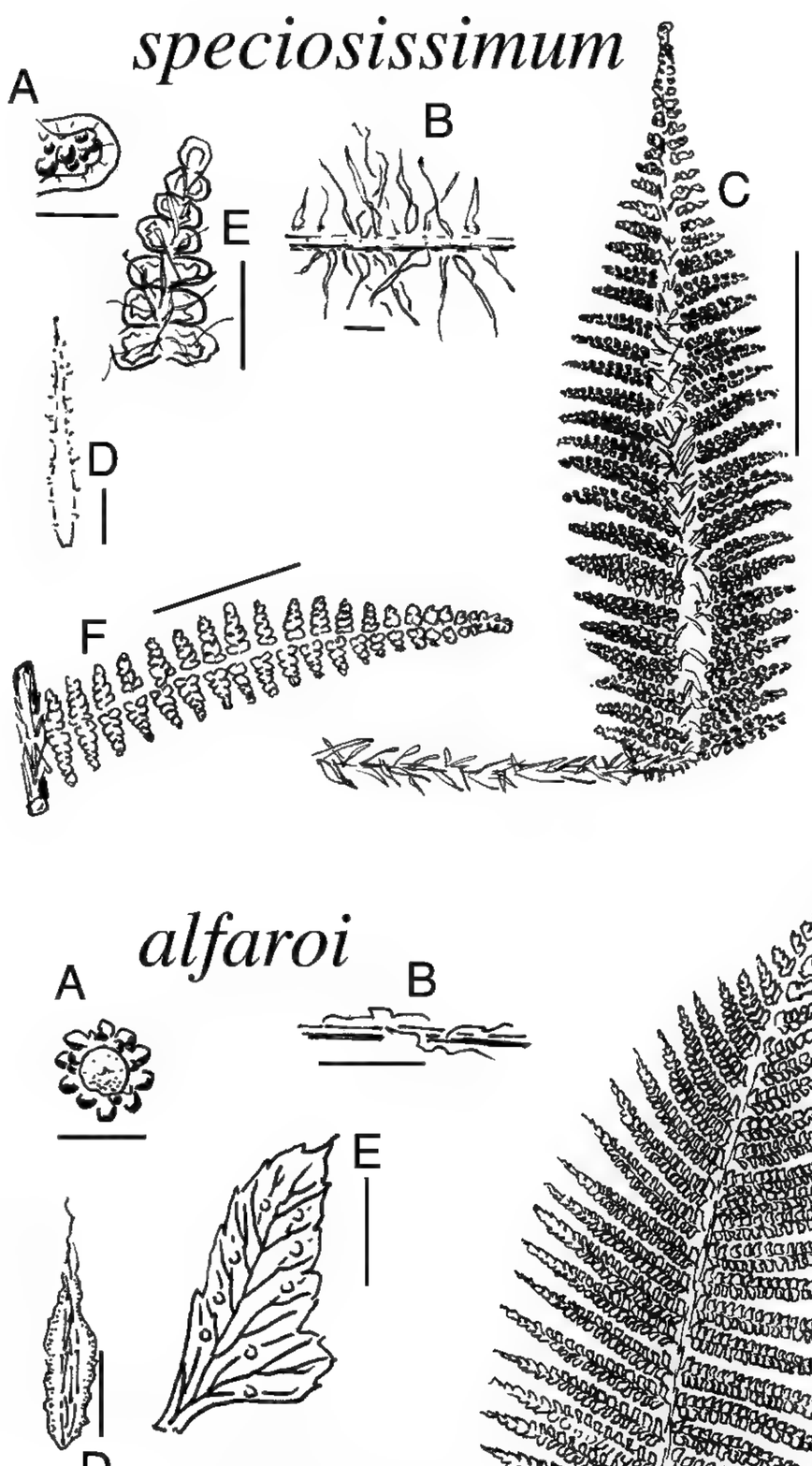


Figure 1. The Costa Rican species of *Polystichum*. *P. platyphyllum* (Willd.) C. Presl. A–G drawn from *D. S. Barrington 1973* (VT). *P. dubium* (H. Karst.) Diels. A, C, D, H, F drawn from *A. Rojas & P. L. Pacheco 5075* (VT). *P. concinnum* Lellinger ex Barrington. A–F drawn from *D. S. Barrington 724* (VT). *P. muricatum* (L.) Fée. A–F drawn from *D. S. Barrington 1240* (VT). *P. lilianiae* Barrington. A–F drawn from *D. S. Barrington 1926* (CR). *P. turrialbae* Christ. A–F drawn from *D. S. Barrington 2050* (VT). —A. Sorus; scale bar = 1 mm. —B. Pinna-rachis scales; scale bar = 1 mm. —C. Leaf; scale bar = 15 cm. —D. Basal petiole scale; scale bar = 5 mm. —E. Medial pinnule; scale bar = 5 mm. —F. Medial pinna; scale bar = 3 cm. —G. Lamina near apex; scale bar = 1 cm. —H. Rachis scales; scale bar = 2 mm.







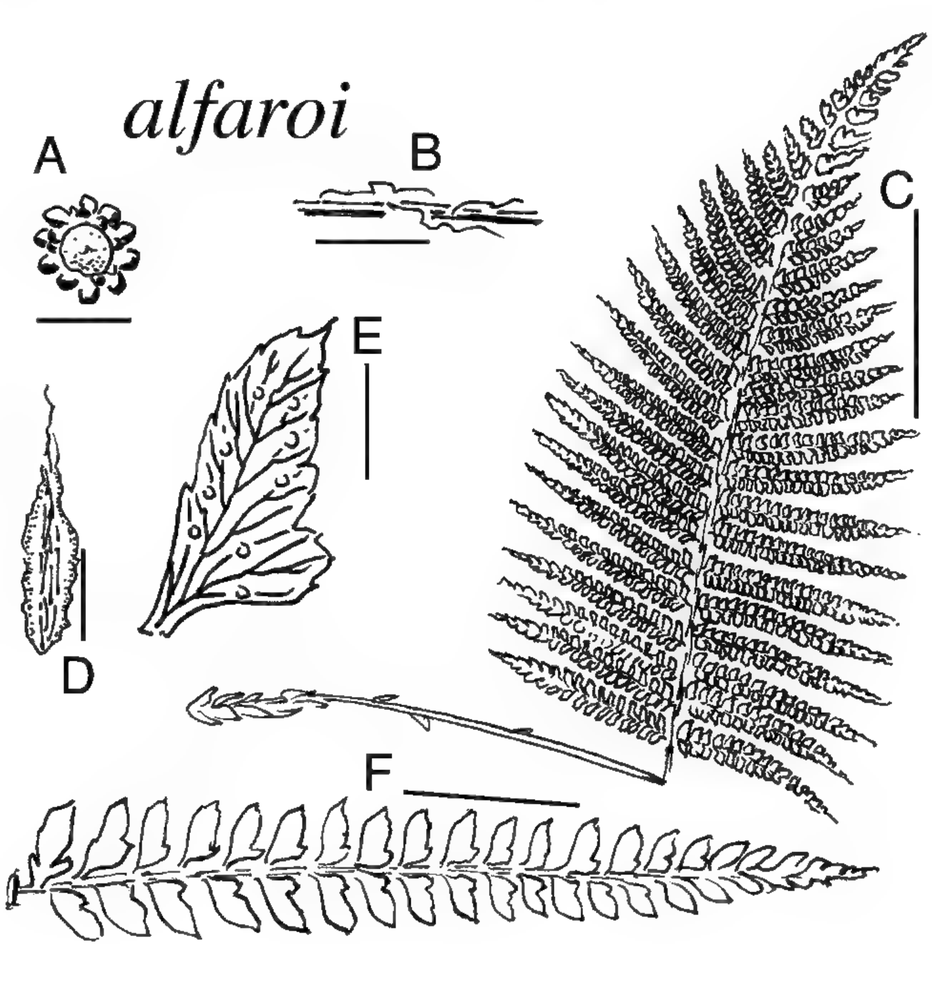


Figure 2. The Costa Rican species of *Polystichum*. *P. alfaroi* (Christ) Barrington. A–F drawn from *D. S. Barrington 1213, 1242* (VT). *P. hartwegii* (Klotzsch) Hieron. A–F drawn from *C. Hamilton & H. Stockwell 3615A* (VT). *P. nudicaule* Rosenst. A–F drawn from *D. S. Barrington 1277, 1555* (VT). *P. orbiculatum* (Desv.) J. Rémy & Fée. A–F, J drawn from *D. S. Barrington 1284* (VT). *P. speciosissimum* (A. Braun ex Kunze) R. M. Tryon & A. F. Tryon. A–F drawn from *D. S. Barrington 977* (VT). *P. talamancanum* Barrington. A–F drawn from *G. Davidse 25034* (VT). —A. Sorus; scale bar = 1 mm. —B. Pinna-rachis scales; scale bar = 1 mm. —C. Leaf; scale bar = 15 cm. —D. Basal petiole scale; scale bar = 5 mm. —E. Medial pinnule; scale bar = 5 mm. —F. Medial pinna; scale bar = 3 cm. —J. Near-apical pinnule; scale bar = 1 mm.

sporangia and true hairs on the surface. The hairs are notable in that hairs are generally not found on tropical American *Polystichum* species, suggesting the release of a silenced hair-production developmental pathway by the gall formation process.

Polystichum concinnum occurs from 1600 to 3400 m in forests and disturbed terrain on the Cordillera Central and the Cordillera de Talamanca as far south as Chiriquí Province in Panama. It is the only large *Polystichum* in the oak-dominated montane rainforests of the Sierra Talamanca, where it is common. In these forests, *P. concinnum* prefers sites that suggest a history of disturbance within the intact forest, such as along stream courses and on earthen banks. The species is especially common in the secondary forest that has grown up on sites disturbed by the construction of roads at higher elevations. *Polystichum concinnum* has an unusually broad elevational distribution. Plants I encountered at ca. 1600 m outside of San Gerardo, at the base of the main foot trail to Cerro Chirripó in disturbed terrain cleared from wet premontane forest, are typical *P. concinnum* both morphologically and genetically. *Polystichum concinnum* also extends above treeline (reaching at least 3400 m) on the Sierra Talamanca in open disturbed sites such as borrow-pit excavations.

Polystichum concinnum is endemic to the Cordillera Central and the Cordillera de Talamanca in Costa Rica and Panama. It is diploid based on meiotic chromosome counts (Barrington, 1990). Morphologically, it most closely resembles Mexican species such as *P. distans* E. Fourn.

Selected specimens examined. COSTA RICA. **Cartago:** Villa Mills, below but in sight of La Georgina, *D. S. Barrington 686* (CR). **Heredia:** 1.7 km NNE of Porrosatí, on Río Ciruelas, 10°06′N, 84°05′W, 2200 m, *D. S. Barrington 1215* (VT). **San José:** Quebrada de los Yases, entre Palmilera & San Joaquín de Dota, 1700 m, *A. Jiménez M. 1475A* (CR, F, NY, US). **San José/Cartago:** near El Trinidad & Km. 72 (20 km SE from Empalme) along Interamer. hwy., 9°40′N, 83°53′W, *W. Burger & R. G. Stolze 5965* (CR, F). PANAMA. **Chiriquí:** Holcomb's trail, 8–10 mi. above El Boquete, Chiriquí, 1400–1550 m, *E. P. Killip 5059* (US).

3. Polystichum dubium (H. Karst.) Diels, Nat. Pflanzenfam. [Engler & Prantl] 1(4): 194. 1899. Basionym: *Phegopteris dubia* H. Karst., Fl. Columb. (H. Karst.) 1: 169, tab. 84. 1861. *Cyrtomium dubium* (H. Karst.) R. M. Tryon & A. F. Tryon, Rhodora 83: 134. 1981. TYPE: Colombia. s.d., *H. Karsten s.n.* (holotype, LE not seen; isotype, B!). Figure 1.

This species is the type of *Polypodium* sect. *Cyrtomiphlebium* Hook., Sp. Fil. 5: 15. 1864.

Rhizome erect, ca. 3 cm diam. Fronds typically 25–40 cm, spreading; petiole scales ca. 1 cm, lanceolate, conform, atropurpureous with a narrow ochraceous edge, the edge sharply distinct from the center, petiole-scale cilia short, stiff, infrequent. Laminae ca. 3 times as long as wide, acute, 1-pinnate and irregularly crenate, without a bulbil; pinnae acuminate and falcate, ca. 3 times as long as wide, barely ascendant, inequilateral but without an auricle, spinules absent, the basal pinnae shorter than the next distal; pinna-rachis scales filiform, ochraceous. Indusia absent.

Discussion. *Polystichum dubium* is unique among Costa Rican polystichums in being strictly once-pinnate. It could be taken as a small *Phanerophlebia* C. Presl; it differs from *Phanerophlebia* in being exindusiate with gradually reduced leaf apices instead of indusiate with conform leaf apices. Neither is it a *Cyrtomium*, which in the strict sense is an Old World genus of indusiate *Polystichum* allies with subconform frond apices and multiple stories of areolae.

Polystichum dubium has been collected at two sites in Costa Rica between 1800 and 2500 m, one from Porrosatí on the Pacific slope of Volcán Barba in the Cordillera Central and the other from Coto Brus on the lower Pacific slopes of the Cerro de Talamanca near Panama. Ecologically this species has a strong preference for the earthen banks of streams in lower montane forests. At the lower limit of its elevational distribution, it shares the stream bank habitat with *P. platyphyllum*. Most of the appropriate habitat is now lost to urbanization in the Valle Central, and the species is lost from the Volcán Barba site.

At the northern limit of its distribution in Costa Rica, the species is known in the Andes from Colombia to Bolivia (Kessler et al., 2005), where *Polystichum dubium* has been found much more frequently than in Costa Rica in recent years. There is no cytological information for this species. The lack of a true indusium and the strong presence in the northern and central Andes suggests that *P. dubium* pertains to the Andean clade.

Selected specimens examined. COSTA RICA. **Heredia:** slopes of Barba, Porrosatí, 2500 m, *W. H. Wagner & F. S. Wagner 79019* (NY); above Porrosatí, slopes of Volcan Barba, 2500 m, *W. H. Wagner & F. S. Wagner 77503* (US). **Puntarenas:** Coto Brus, Zona Protectora Tablas, Sendero Sur, 1900–2000 m, 8°57′03″N, 82°45′03″W, *A. Rojas & P. L. Pacheco 5075* (VT).

4. Polystichum hartwegii (Klotzsch) Hieron., Hedwigia 46: 355. 1907, as "hartwigii." Basionym: *Aspidium hartwegii* Klotzsch, Linnaea 20: 366–367. 1847. TYPE: Guatemala. Las Nubes mtn.,

near Guatemala City, 1839–1840, *K. T. Hartweg 631* (holotype, B not seen; isotypes, BM!, K!, P not seen). Figure 2.

Polystichum drepanoides E. Fourn., Mexic. Pl. 1: 92. 1872. TYPE: Mexico. "inter San Bartolo et Pueblo-Novo," s.d., *J. J. Linden s.n.* (holotype, P not seen, P photo at US!).

Aspidium trejoi Christ, Bull. Herb. Boissier, sér. 2, 5: 255. 1905, as "Trejoi." TYPE: Mexico. Chiapas: San Pablo, 2000 m, *G. Münch 167* (lectotype, designated by A. R. Smith [1981: 197], P not seen; isolectotype, DS!).

Rhizome erect, to at least 4 cm diam. Fronds to 80 cm, spreading; petiole scales ca. 2 cm, narrow-lanceolate, conform, fuscous with a fulvous edge, the edge sharply distinct from the center, petiole-scale cilia short and broad, infrequent. Laminae ca. 3.5 times as long as wide, 2-pinnate and crenate to usually 2-pinnate pinnatifid, acuminate, without a bulbil; pinnae attenuate, ca. 5(to 7) times as long as wide, attached at right angles to the rachis, the basal pinnae barely shorter than the next distal or the same length; pinna-rachis scales filiform, amber; pinnules flat, obliquely attached especially distally, the auricle weakly developed, the apex blunt, spinules well-developed, the basal acroscopic pinnule of the medial pinnae longer than the adjacent pinnule. Indusia 1 mm or more in diam.

Discussion. *Polystichum hartwegii* has a unique combination of large indusia and filiform pinna-rachis scales. There is extensive superficial variation in pinna and pinnule shape and size in *P. hartwegii*, which is one of the reasons for the number of synonyms.

Polystichum hartwegii occurs at 1200–2300 m in lower montane and premontane moist to wet forests and areas cleared from them on the Cordillera de Talamanca. However, there are few recent collections. This species is among the most widely distributed of the New World tropical group, extending from southern Mexico to Bolivia (Kessler et al., 2005). In Guatemala, the species has been encountered at unexpectedly high elevations (up to 2900 m, *T. S. Quedensley 659*, VT!).

The two syntypes of *Aspidium trejoi* that remained after the earlier designation of the lectotype from Mexico (Smith, 1981: 197) are both Costa Rican collections, which pertain to at least three species, only one of which is *Polystichum hartwegii*. I have seen the following: Costa Rica, San José Province, El Copey, Bords du Río Pedregoso, 1800 m, *Tonduz 11853* (CR! [det. *P. alfaroi*], US 365951!, US 830938! [det. *P. concinnum*]); Copey, *Tonduz 11894* (CR! [det. *P. hartwegii*]).

Selected specimens examined. COSTA RICA. **Cartago:** mtns. above Tres Ríos, 5000 ft., *E. Scamman & L. R. Holdridge 7944* (GH, US). **Limón:** Cordillera de Talamanca, Atlantic slope, canyon of Río Siní, 1800–1900 m, 09°13′N, 82°59′W, *G. Davidse & G. Herrera Ch. 29118* (VT). **San José:** forêts du Copey, 1800 m, *A. Tonduz 11894* (BM, CR, US).

5. Polystichum lilianiae Barrington, Brittonia 55: 321, fig. 2. 2003, as "lilianae." TYPE: Costa Rica. Cartago: Villa Mills, Km. 95 on Pan American Hwy., 3100 m, 15 Jan. 1993, *D. S. Barrington 2042* (holotype, VT!; isotypes, NY!, UC!). Figure 1.

Rhizome erect, ca. 2 cm diam., supported by adventitious roots. Fronds typically ca. 50 cm, spreading; petiole scales ca. 1 cm, lanceolate, fuscous with a broad stramineous edge, the edge sharply distinct from the center, petiole-scale cilia short, stiff, frequent. Laminae at most 3 times as long as wide, acuminate, 2-pinnate and serrate, without a bulbil; pinnae attenuate, ca. 6 times as long as wide, attached at right angles to the rachis, the basal pinnae the longest; pinna-rachis scales lanceolate, ochraceous; pinnules flat, attached at oblique angles throughout, the auricle weakly developed, the apex acute, spinules well-developed, the basal acroscopic pinnule of the medial pinnae longer than the adjacent pinnule. Indusia ca. 1 mm in diam.

Discussion. *Polystichum lilianiae* is one of two montane rainforest *Polystichum* species in Costa Rica with small leaves and thin rhizomes; the other is *P. turrialbae*. The two are compared below, in the treatment of *P. turrialbae*. *Polystichum lilianiae* sometimes has anomalous foliage, with the pinnules distorted and reduced.

Polystichum lilianiae is endemic to the Cordillera Central and the Cordillera de Talamanca in Costa Rica; it may be expected in contiguous montane regions in Panama. It is occasional in montane rainforests dominated by *Quercus* L. species from 2500 to 3000 m.

Polystichum lilianiae is an allotetraploid with *P. turrialbae* as one of its progenitors (Barrington, 2003). The other progenitor is unknown, but judging from the differences between *P. turrialbae* and *P. lilianiae*, the second progenitor should be a species with dark petiole scales, fairly small (ca. 0.6 mm) indusia, the basal pinnae broadest, and pinnule attachment strongly oblique. Given its morphology, this species appears to be a fertile hybrid combining the heritage of two different species of the Mayan clade.

Selected specimens examined. COSTA RICA. **Cartago:** Villa Mills, S of La Georgina, NNE of hwy. across from first

borrow pit, *D. S. Barrington 677, 679* (CR, VT); Villa Mills, in dense thicket in oak forest below & just W of Hotel La Georgina at Km. 95 on Pan Amer. Hwy., *D. S. Barrington 1926* (CR). **Heredia:** NE slope Volcán Barva, betw. Laguna del Barva & base of Caños las Marías, 2450–2800 m, 10°08.5′N, 84°07′W, *M. Grayum 7455* (CR).

6. Polystichum muricatum (L.) Fée, Mém. Foug. 5. Gen. Filic. 278. 1852. Basionym: *Polypodium muricatum* L., Sp. Pl. 2: 1093. 1753. TYPE: tab. 1, fig. 6, Petiver, Pter. Amer. 53. 1712 (lectotype, designated by Proctor [1985: 460, tab. 1, fig. 6], Petiver [1712]). Figure 1.

Aspidium moritzianum Klotzsch, Linnaea 20: 367. 1847. TYPE: Venezuela. Aragua: Colonia Tovar, *J. W. K. Moritz 280* (holotype, B not seen; isotypes, GH!, K!).

Rhizome ascendant, ca. 2 cm diam. Fronds commonly 60–90 cm, spreading; petiole scales ca. 1 cm, lanceolate, conform, fuscous with a narrow fulvous edge, the boundary between edge and center indistinct, petiole-scale cilia absent. Laminae ca. 4 times as long as wide, acuminate, 2-pinnate pinnatifid, without a bulbil; pinnae attenuate, ca. 5 times as long as wide, attached at right angles to the rachis; the basal pinnae barely if at all shorter than the next distal; pinna-rachis scales linear, fulvous; pinnules flat, attached at right angles throughout, the auricle weakly developed, the apex rotund, spinules well-developed, the basal acroscopic pinnule of the medial pinnae longer than the adjacent pinnule. Indusia ca. 0.3 mm in diam.

Discussion. The combination of very small indusia and petiole scales that totally lack cilia is unique to *Polystichum muricatum*. The relatively thin-textured lamina, the linear pinna-rachis scales, and the unique apex shape of the pinnules (rotund with a well-developed spinule) help in identification as well.

Known from Cerros de la Carpintera, the Cordillera Central, Cerro de Talamanca (Cerros de Escazú region), and the Cordillera de Guanacaste at 1000–2700 m elevation, *Polystichum muricatum* is occasional in intact forests and secondary growth, predominantly in premontane wet forests.

A broad-ranging tropical American species, *Polystichum muricatum* is known throughout Central America (although missing from Guatemala), the Greater Antilles, and from Venezuela (*J. Mostacero et al. 88*, VT!) to Ecuador (*D. S. Barrington 1062*, VT!). This broad concept of *P. muricatum* needs testing with modern genetic tools. The species is diploid, based on counts from Mexico (Mickel et al., 1966; Smith & Mickel, 1977). Phylogenetically, Costa Rican *P. muricatum* is a member of the Mayan clade.

Selected specimens examined. COSTA RICA. **Cartago:** Cerro de la Carpintera, 1500–1850 m, *P. C. Standley 35767* (US); Cerros de la Carpintera, end near Boy Scout Camp, 9°54′N, 83°59′W, *D. S. Barrington 1228* (CR); along rd. to Planta Eléctrica María del Rosario, near Río Tiribí, NE of Tres Ríos, 9°57′N, 83°58′W, 1750 m, *M. H. Grayum & P. Sleeper 3308* (MO, UC). **Puntarenas:** Monteverde, beginning of rd. to San Luis, coppice in cow pasture, 1450 m, *D. P. Little & D. S. Barrington 349* (VT). **San José:** Cerro de Piedra Blanca, above Escazú, *P. C. Standley 32511* (US).

7. Polystichum nudicaule Rosenst., Repert. Spec. Nov. Regni Veg. 11: 56. 1912. TYPE: Bolivia. Nor Yungas: "Yungas septentrionalis," Unduavi, 3400 m, *O. Buchtien 2658* (lectotype, designated here, US!; isolectotype, UC!). Figure 2.

Rhizome erect, ca. 1 cm diam. *Fronds* to 45 cm, spreading (erect in full sun). Petiole scales ca. 1.5 cm, broad-lanceolate, conform, atropurpureous, petiole-scale cilia both short and stiff and long and delicate, frequent distally on the scales. Laminae 2 to 3 times as long as wide, long-attenuate, 2-pinnate and crenate, without a bulbil. Pinnae attenuate, ca. 5 times as long as wide, attached at right angles to the rachis; the basal pinnae as long as or longer than the more distal. Pinna-rachis scales long-lanceolate, ferrugineous. Pinnules revolute (flat in deep shade), attached at slightly oblique angles throughout, the auricle poorly developed, the apex acute, spinules weak (irregularly developed), the basal acroscopic pinnule of the medial pinnae barely longer than the adjacent pinnule. Indusia absent.

Discussion. *Polystichum nudicaule* in Costa Rica is a páramo *Polystichum* with long-attenuate blades that are broadest at the base and pinnules that are attached to the pinna-rachis at a slightly oblique angle. In addition, the rachis has many more narrow-lanceolate, atropurpureous scales than *P. talamancanum*, a frequent companion in the páramo. The pinnules are strongly revolute in sun but flat in shaded locations (Barrington, pers. obs.).

Polystichum nudicaule has been found so far in Costa Rica only on the Cerro de la Muerte, Cordillera de Talamanca, at ca. 3400 m, but it is to be expected in the high páramos of the Chirripó massif. At the Cerro de la Muerte it grows above treeline in sheltered areas, both in stream beds and among páramo shrubs and treelets, where the taxon may be easily overlooked as it resembles *P. talamancanum* juveniles, which differ in their narrow-based blades with acute or at most short-attenuate tips. The extreme forms with small leaves and revolute pinnules resembling the Bolivian lectotype of *P. nudicaule* are found among páramo vegetation in full sun.

Polystichum nudicaule is found from Costa Rica to Bolivia (Kessler et al., 2005). In the Central Andes it is common in high-elevation forests and páramos. Ploidy is unknown. It is probably a member of the Andean clade—since it is exindusiate, it is in the same clade as the Central Andean *P. montevidense* (Spreng.) Rosenst. in molecular analysis (Driscoll & Barrington, 2007)—and it is found only in Costa Rica outside the Central Andes. In my previous work, I included *P. nudicaule* in a broadly defined *P. lehmannii* Hieron., but the two are distinct enough to merit recognition as separate species, following Kessler et al. (2005). *Polystichum lehmannii* has spinules well-developed on the pinnules, not confined to auricle and apex or absent. In addition, *P. lehmannii* has pinna-rachis scales with a yellow hue (they are amber to fulvous), whereas *P. nudicaule* has pinna-rachis scales with a reddish hue (they are typically ferrugineous in Costa Rica).

Remaining syntypes are also from the type locality in Bolivia and include three other collections by Buchtien: *O. Buchtien 2657* (syntype, B not seen; isosyntype, US!), *O. Buchtien 2659* (isosyntype, US!), *O. Buchtien 2662* (not seen).

Selected specimens examined. COSTA RICA. **San José:** Cordillera de Talamanca, Buenavista-Massiv, Cerro Páramo, Westhang, 3275 m, *H. Kuhbier & L. D. Gómez P. 298* (CR); SE of towers, Cerro de la Muerte, *D. S. Barrington 975* (VT); shady niches on wall of deep stream course cut into páramo, area of transmission towers, Cerro de la Muerte, *D. S. Barrington 1964* (CR); area of towers at summit of Cerro de la Muerte, 3400 m, *D. S. Barrington 2137* (VT).

8. Polystichum orbiculatum (Desv.) J. Rémy & Fée, Fl. Chil. [Gay] 6: 515. 1853. Basionym: *Aspidium orbiculatum* Desv., Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 5: 321. 1811. TYPE: "in America australi," [*A. N. Desvaux s.n.*] (holotype, P!). Figure 2.

Nephrodium polyphyllum C. Presl, Reliq. Haenk. 1: 37. 1825. TYPE: "Habitat in Peruvia? In Chile?," *T. Haenke s.n.* (holotype, PR!).

Nephrodium trapezoides C. Presl, Reliq. Haenk. 1: 37. 1825, non *Polystichum trapezoides* (Sw.) C. Presl, Tent. Pterid. 83. 1836. TYPE: Peru. "in montanis Peruviae," *T. Haenke s.n.* (holotype, PR not seen; isotype, K!).

Polypodium rigidum Hook. & Grev., Icon. Filic. 2: t. 163. 1831. TYPE: Peru. "Ad verticum montis Pichincha," *W. Jameson s.n.* (holotype, K!), non P. rigidum Aubl., Hist. Pl. Guiane 2: 963. 1775.

Polypodium saxatile Klotzsch, Linnaea 20: 383. 1847. TYPE. Peru. "[A]d Diezmo in locis umbrosis, saxosis," *H. Ruiz L. 65* (holotype, B!).

Polystichum pumilio Maxon, J. Wash. Acad. Sci. 19: 197, fig. 1. 1929. TYPE: Ecuador. Chimborazo: Urbina, 3475 m, 22–28 Oct. 1923, *H. E. Anthony & G. H. H. Tate 394* (holotype, US-01424988!). [The species epithet, a noun in apposition, should stand as originally coined.]

Polystichum pygmaeum Copel., Univ. Calif. Publ. Bot. 19: 300, tab. 56. 1941. TYPE: Bolivia. [La Paz:] 13 km S of Tiahuánaco, 4200 m, 31 Mar. 1936, *J. West UC Exped. 6393* (holotype, UC-602775!).

Rhizome erect, ca. 3 cm diam. Fronds to 65 cm, stiffly erect; petiole scales ca. 1 cm, broad-lanceolate, conform, rufous, petiole-scale cilia long and delicate, frequent. Laminae ca. 9 times as long as wide, attenuate, 2-pinnate and crenate (basal pinnules of the pinnae sometimes pinnatisect), without a bulbil; pinnae acute, ca. 6 times as long as wide, strongly ascendant except in shade; the basal pinnae longer than the next distal. Pinna-rachis scales lanceolate, rufous; pinnules strongly revolute except in shade, attached at right angles throughout, the auricle weakly developed, the apex blunt, spinules weak (the pinnule apex without a single well-developed spinule), the basal acroscopic pinnule of the medial pinnae longer than the adjacent pinnule. Indusia absent.

Discussion. *Polystichum orbiculatum* is a páramo species with extremely narrow leaves, strongly ascendant pinnae, and rufous scales. Above treeline in Costa Rica, there are two stiffly erect, twice-pinnate polystichums that routinely grow in full sun, *P. orbiculatum* and *P. talamancanum*. The latter is much more common and differs in having fuscous petiole scales, longer pinnae, and pinnules with a strong apical spinule. *Polystichum orbiculatum* varies remarkably with habitat; shade forms are flat and lax while sun forms are rigidly erect with strongly revolute pinnules. High-elevation individuals are dwarfed as well. This variation explains the large number of names that have been coined for the species.

In Costa Rica, *Polystichum orbiculatum* is known only from the Cerro de Talamanca, where it grows in páramos and open, disturbed areas from 3100 to 3800 m. While this species is only rarely found below 3400 m, in contrast, the similar *P. talamancanum* descends below treeline to ca. 3000 m on road cuts.

Polystichum orbiculatum s.l. is widespread in tropical America, collected from Mexico (Mickel & Smith, 2004) to Bolivia (Kessler et al., 2005); it is absent in the West Indies. It is a tetraploid species based on counts from Costa Rica (Barrington, 1990), but small-spored individuals from the northern Andes suggest that the taxon in the broad sense as here construed includes at least one of its progenitors (Barrington et al., 1986).

Selected specimens examined. COSTA RICA. **San José:** summit of Cerro de la Muerte, S side of northern-most

summit with radio towers, 9°33′34″N, 83°45′13.5″W, *D. S. Barrington 1284* (CR); trail Valle de los Leones, lower part of Valle de los Conejos, Río Talari [Cerro Chirripó], 9°27′N, 83°31′W, 3400 m, *W. C. Burger & L. D. Gómez P. 8308* (F, NY); Cerro Chirripó massif; area betw. Refugio & lake at head of Río Dtikebi, 3500 m, *G. Davidse & R. W. Pohl 1548* (MO); Cerro de la Muerte, Cordillera de Talamanca; 3100–3400 m, *A. F. Skutch & M. Barrantes 5192* (MO).

9. Polystichum platyphyllum (Willd.) C. Presl, Tent. Pterid. 84. 1836. Basionym: *Aspidium platyphyllum* Willd., Sp. Pl., ed. 4 [Willdenow] 5(1): 255. 1810. TYPE: Venezuela. "Habitat ad Caracas in montosis nemorosis," *F. Bredemeyer s.n.* (holotype, B-W 19789!). Figure 1.

Polystichum opacum Rosenst., Hedwigia 46: 112. 1906. TYPE. Brazil. Rio Grande do Sul: Mun. Rio Pardo, Fazenda Soledade, 1904, *C. Jürgens 42* (lectotype, designated here, B not seen; isolectotypes, NY!, UC 441761!).

Rhizome ascendant, ca. 2 cm diam., supported by adventitious roots. Fronds to 60 cm, wide-spreading; petiole scales ca. 1 cm, lanceolate, conform, fulvous to stramineous, petiole-scale cilia short. Laminae ca. 2.5 times as long as wide, long-attenuate, 2-pinnate and crenate, with a subapical bulbil; pinnae acuminate, ca. 4 times as long as wide, attached at right angles to the rachis; the basal pinnae about the same length as the next distal. Pinna-rachis scales filiform, fulvous; pinnules flat, attached at slightly oblique angles throughout, the auricle weakly developed, the apex blunt, spinules weak (developed only at apex and auricle), the basal acroscopic pinnule of the medial pinnae longer than the adjacent pinnule. Indusia absent.

Discussion. *Polystichum platyphyllum* is unmistakable: even when the subapical leaf bulbil is missing, the long-attenuate, once-pinnate leaf apex is unique among Costa Rican polystichums. In addition, the other twice-pinnate polystichums from middle and lower elevations are all indusiate. In living plants, the leaf apex, from the area of the bulbil distally, is bent so that it is parallel to the ground. In the field, the leaves have a lustrous green texture above. As the name implies, the pinnules are consistently flat, never recurved at all.

This species is known from the Cordillera de Tilarán, the Cordillera Central, and the Cordillera de Talamanca at elevations from 600 to 1500 m. This is the lowest elevation preference of any *Polystichum* in Costa Rica. *Polystichum platyphyllum* characteristically grows on soil banks in premontane wet and rainforests; these soil banks are usually near streams, and the plants are often encountered directly over flowing water. This habitat preference is shared only with the once-pinnate and bulbless *P. dubium* in Costa Rica. *Polystichum platyphyllum* is not commonly encountered in Costa Rica; a number of historical localities (e.g., on the Río Torres in San José) have been destroyed by human activity.

Polystichum platyphyllum is perhaps the most widely distributed *Polystichum* species in tropical America: it is known from Mexico (*D. S. Barrington 2029*, VT!) to Bolivia (*P. G. Windisch 2373*, VT!) as well as Brazil and Argentina (*E. R. de la Sota 4076*, US!), and it is also found in the West Indies (Mickel, 1997). Perhaps the taxon's preference for lower-elevation stream banks explains its wide distribution. Its closest allies are probably among species of the Andean clade, since it is sister to the Central Andean *P. montevidense* in molecular analysis (Driscoll & Barrington, 2007) and lacks an indusium. *Polystichum platyphyllum* is diploid, based on a count from Mexico (Smith & Mickel, 1977).

Remaining syntypes of *Polystichum opacum* are from the type locality in Rio Grande do Sul and include two other Jürgens collections: *C. Jürgens 71* (B not seen); 1 Sep. 1904, *Jürgens 235* (B not seen; isosyntype, UC 441760!).

Selected specimens examined. COSTA RICA. **Alajuela:** alrededores de San Ramón, NO lado, *A. M. Brenes 15320*, *15341* (CR). **Heredia:** Barba, foot of Volcán Barba, 1100 m, *E. Scamman 7082* (GH, US). **Puntarenas:** Sierra de Tilarán, Monteverde, *C. W. Palmer 154* (CR, NY). **San José:** Finca Fortuna, Desamparados, 3800 ft., *E. Scamman & L. R. Holdridge 7943* (GH, US); basin of El General, 675–900 m, *A. F. Skutch 5207* (MO, NY, UC).

10. Polystichum speciosissimum (A. Braun ex Kunze) R. M. Tryon & A. F. Tryon, Rhodora 83: 136. 1981. Basionym: *Cheilanthes speciosissima* A. Braun ex Kunze, Analecta Pteridogr. 35, tab. 23. 1837. *Plecosorus mexicanus* Fée, Mém. Foug., 5 Gen. Fil. 150, pl. 13A, fig. 1. 1852, nom. superfl. *Plecosorus speciosissimus* (A. Braun ex Kunze) T. Moore, Index Fil. [T. Moore], xl. 1857. TYPE: Mexico, Sep. 1827, *W. F. Karwinski* (holotype, LZ not seen; isotype, B!). Figure 2.

This species is the type of the genus *Plecosorus* Fée, Mém. Foug., 5 Gen. Fil. 150, Pl. 13, 1850–1852.

Plecosorus mexicanus is a renaming of *Cheilanthes speciosissima*, based on the type of that name.

Rhizome erect, ca. 8 cm diam. Fronds to 90 cm, erect-ascending; petiole scales ca. 2.5 cm, long-lanceolate, conform, orange, petiole-scale cilia mostly short and broad (some long and delicate). Laminae 3 to 4 times as long as wide, acuminate, 2-pinnate pinnatisect, without a bulbil; pinnae attenuate, ca.

4.5 times as long as wide, attached at right angles to the rachis; the basal pinnae barely shorter than the next distal; pinna-rachis scales narrow-lanceolate, rufous; pinnules strongly revolute, attached at right angles throughout, the auricle weakly developed, the apex blunt, spinules absent (pinnule margins lacerate, scarious), the basal acroscopic pinnule of the medial pinnae longer than the adjacent pinnule. Indusia absent (false indusium present).

Discussion. The unmistakable *Polystichum speciosissimum* is one of the showpieces of the Costa Rican páramo. The highly dissected leaves, unusually pale for *Polystichum*, form a steeply ascending rosette approaching a meter high, and the mass of brilliant orange scales at the petiole bases is unique. The undersides of the young leaves are also covered with orange scales; these fade to white with age. The pinnae are often curved downward in the plane of the leaf toward the ground. Old individuals build thick trunks some 20 cm high. *Polystichum speciosissimum* has a discrete hyaline edge to the ultimate segments; that is, it has a false indusium reminiscent of the Pteridaceae, hence its taxonomic inauguration in *Cheilanthes* Sw.

Restricted to páramos in Costa Rica, *Polystichum speciosissimum* is found in the Cerro de Talamanca, including the Cerro de la Muerte and Cerro Chirripó, from 3100 to 3800 m. This species often has brown necrotic areas on the leaves, apparently the result of frost damage.

Polystichum speciosissimum has a disjunct distribution between the Sierra Talamanca and the mountains of Mexico and Guatemala (documented for the latter by Stolze [1981]). Isozyme data reveal the Costa Rican populations to be a genetically depauperate subset of those in northern Mesoamerica, suggesting recent dispersal from north to south (Barrington, 2005). It is diploid, based on counts from Costa Rica (Barrington, 1990). *Polystichum speciosissimum* is sister to the remainder of the continental tropical American polystichums so far analyzed, suggesting that it originated early in the history of the Neotropical clade (Driscoll & Barrington, 2007). Its geography points to a northern origin for the clade. As it is deeply nested within *Polystichum* (Driscoll & Barrington, 2007), there is no basis for recognizing *P. speciosissimum* as a separate genus, in spite of its distinctive morphology.

Selected specimens examined. COSTA RICA. **Cartago:** Cerro de la Muerte, roadcut N side of Pan American Hwy. betw. high point in rd. & first dwellings, ca. 3300 m, *D. S. Barrington 812a* (VT). **San José:** area of towers at summit of Cerro de la Muerte, 3400 m, *D. S. Barrington 2149* (CR); same locality, *D. S. Barrington 2150* (VT).

11. Polystichum talamancanum Barrington, Ann. Missouri Bot. Gard. 76: 369, f. 2. 1989. TYPE: Costa Rica. Cartago: highest point on Pan-American Hwy., Cerro de la Muerte, 3330 m, 4 Jan. 1980, *D. S. Barrington 708* (holotype, GH!; isotypes, CR!, VT!). Figure 2.

Rhizome erect, ca. 8 cm diam. Fronds to 100 cm, stiffly erect; petiole scales ca. 1.5 cm, long-lanceolate, conform, fuscous, petiole-scale cilia both short and stiff and long and delicate. Laminae ca. 5 times as long as wide, acuminate to attenuate, 2-pinnate and serrate, without a bulbil; pinnae acuminate (to attenuate), 4 to 5 times as long as wide, strongly ascendant; the basal pinnae at least as long as the next distal; pinna-rachis scales narrow-lanceolate, fulvous to ochraceous; pinnules strongly revolute, attached at right angles throughout, the auricle prominent, the apex acute, spinules well-developed (pinnule apex with a single well-developed spinule), the basal acroscopic pinnule of the medial pinnae longer than the adjacent pinnule. Indusia absent (occasionally weakly developed proximally on the pinnae).

Discussion. In its typical habitat on open páramo, *Polystichum telamancanum* is a stiffly erect *Polystichum* with dark, long-ciliate petiole scales and pointed, revolute pinnules. Rarely, it has partially developed indusia, especially on the pinnules nearest the rachis. This species also grows in shady sites above treeline, where the pinnules are nearly flat. These shade-form plants are easily confused with the much less common *P. nudicaule*, where they grow together; *P. talamancanum* differs in having blades that are broadest above the base and pinnules attached at right angles to the pinna-rachis. *Polystichum talamancanum* is notable for precociously fertile individuals, including *Barrington 583* (CR), which has a fertile lamina only 15 cm long.

Polystichum talamancanum is a common and prominent plant of the Cordillera de Talamanca, where it grows in páramos and in disturbed sites in the montane rainforests from 3000 to 3400 m. It is the most tolerant of high insolation and cold of the polystichums, judging from the frequency and excellent condition of the plants in exposed, apparently high-water-stress sites in the páramo. I have seen hummingbirds gathering rachis scales from this species, presumably to line their nests.

Endemic to Costa Rica and Panama, this allotetraploid (Barrington, 1990) apparently originated recently in these mountains. One progenitor is the endemic *Polystichum concinnum*; another is an unknown taxon also involved in the origin of *P.*

orbiculatum (Barrington, 1990). It seems likely that this species is unique in combining the genetic heritage of the Mayan clade and Andean clade.

Selected specimens examined. COSTA RICA. **Cartago:** Villa Mills, 1.0 km N of Restaurant La Georgina, *D. S. Barrington 577* [shade form] (CR). **Limón:** Cordillera de Talamanca, peak of Cerro Kámuk, 9°16′30″N, 83°02′W, 3350–3549 m, *G. Davidse 26008* (CR, MO). **San José:** Cerro de la Muerte, summit of Cerro de la Muerte, "ox-trail," off side of rd. to transmission towers, *D. S. Barrington 1285* (CR). **San José/Cartago:** Cerro de la Muerte, roadcut; vertical rockface, *D. S. Barrington 583* (CR); páramo region, Cerro de la Muerte, Cordillera de Talamanca, 3100 m, *L. O. Williams 24476* (F, NY, US); Cerro Chirripó, SW slopes, along trail from Canaán to summit, near la caverna, 9800–10,300 ft., *A. M. Evans, D. B. Lellinger & F. Bowers 110* (MO, US).

12. Polystichum turrialbae Christ, Bull. Herb. Boissier, sér. 2, 6: 163. 1906. TYPE: Costa Rica. Heredia: Volcán Turrialba, 1905, *K. Wercklé s.n.* (holotype, P!). Figure 1.

Polystichum smithii Mickel & Beitel, Mem. New York Bot. Gard. 46: 315. 1988. TYPE: Mexico. Oaxaca: summit of Cerro San Felipe, 18 km N of Rte. 175, 9500 ft., *J. T. Mickel 7056* (holotype, NY!).

Rhizome erect, ca. 2 cm diam., supported by adventitious roots. Fronds typically ca. 60 cm but reaching 90 cm, spreading; petiole scales ca. 1 cm, lanceolate, conform, stramineous or stramineous with a weakly developed fulvous center, the boundary between edge and center indistinct, petiole-scale cilia short, stiff, frequent. Laminae about twice as long as wide, acuminate, 2-pinnate and serrate, without a bulbil; pinnae acuminate, ca. 6 times as long as wide, attached at right angles to the rachis; the basal pinnae shorter than the next distal; pinna-rachis scales long-lanceolate, ochraceous; pinnules flat, attached at right angles throughout, the auricle poorly developed, the apex acute, spinules well-developed, the basal acroscopic pinnule of the medial pinnae longer to much longer than the adjacent pinnule. Indusia over 1 mm in diam.

Discussion. *Polystichum turrialbae* is one of two high-montane forest *Polystichum* species in Costa Rica with small leaves and thin rhizomes; the other is *P. lilianiae*. In both species, the rhizomes are erect-ascending and supported by adventitious roots. The leaves of *P. turrialbae* are less lustrous than those of *P. lilianiae*, and the basal pinnae are shorter than the next distal pair rather than longer. The petiole scales without a sharply demarcated central dark stripe also distinguish this species from *P. lilianiae*. The similar *P. fournieri* A. R. Sm. is endemic to montane rainforests of southern Mexico and western Guatemala. Formerly, the name *P. fournieri* was used for all of these species, including all Costa Rican plants, so the name is common on Costa Rican specimens but never (so far) correct. One feature distinguishing both of the species in Costa Rica from the Mexican *P. fournieri* is the droop-tip versus regularly uncoiling vernation, respectively, of the two.

Polystichum turrialbae is a fairly common species growing at 2700–3200 m in oak forests of the Cordillera Central and the Cordillera de Talamanca in Costa Rica. The species is widely distributed from Mexico (Barrington, 1995; Mickel & Smith, 2004) to Bolivia (Kessler et al., 2005). *Polystichum turrialbae* is diploid (Barrington, 2003); it is likely to lie in the indusiate Mayan clade based on its morphology.

Selected specimens examined. COSTA RICA. **Cartago:** Fila Div., Cuericí, 2800 m, *L. D. Gómez P. 2378* (DS, F, GH, NY, US). **Heredia:** N of Heredia, ca. 1 km beyond Porrosatí, in ravine, 2100 m, *D. B. Lellinger & J. J. White III 1680* (F, US). **Limón:** Cordillera de Talamanca, headwaters of unnamed W branch of Río Teribe, betw. Río Sini & continental divide at Cerro Bekom, 9°10′45″N, 83°03′30″W, 2500–2600 m, *G. Davidse, G. Herrera Ch. & R. H. Warner 25740* (CR), *25761* (CR, UC). **San José:** Villa Mills, S of Pan American Hwy. about 1 km E of Hotel La Georgina, *D. S. Barrington 696* (CR).

HYBRIDS

Polystichum concinnum Lellinger ex Barrington × **P. speciosissimum** (A. Braun ex Kunze) R. M. Tryon & A. F. Tryon.

This hybrid is fairly common above treeline on the Cerro de Talamanca in Costa Rica; I have encountered it repeatedly on Cerro de la Muerte. It combines the pale green lamina and paler indument of *Polystichum speciosissimum* with the less dissected lamina of *P. concinnum*; it is at least somewhat revolute. *Barrington 705* (VT), the first documented plant of this hybrid, was a large plant when I first collected material from it in 1979, and it remains alive and prosperous as of 2011, having attained an age of at least 32 years.

Selected specimens examined. COSTA RICA. **Cartago:** Cerro de la Muerte, roadcut on Pan American Hwy. near treeline, *D. S. Barrington 705* (CR, VT). **San José:** Cerro de la Muerte, summit with radio towers, 3400 m, 9°33.5′N, 83°45.2′W, *D. S. Barrington 1274* (VT).

Polystichum concinnum Lellinger ex Barrington × **P. talamancanum** Barrington

This is the commonest of the hybrids encountered in Costa Rica. It is regularly found between 3000 and 3400 m along the Pan American Highway on the Cerro de la Muerte. The pinnae are ascendant like

Polystichum talamancanum but barely revolute and much longer. The true indusia are better developed than in *P. talamancanum*, though still variously vestigial (see Barrington, 1985).

Selected specimens examined. COSTA RICA. **Cartago:** Villa Mills, 0.5 km N of Restaurant La Georgina, 3200 m, *D. S. Barrington 574* (CR, VT). **San José:** Talamanca Range, Rte. 2, Villa Mills, 0–1 km NW of Restaurant La Georgina, Km. 95, 3100–3200 m, *S. R. Hill 17521* (VT).

Polystichum orbiculatum (Desv.) J. Rémy & Fée × **P. talamancanum** Barrington

Documented once using cytology and isozymes (Barrington, 1990), this hybrid strongly resembles *Polystichum orbiculatum*, but its pinnules are acuminate with a single strong spinule at the tip, as in *P. talamancanum*.

Specimen examined. **San José:** Cerro de la Muerte, S side of N summit with radio towers, 9°33′34″N, 83°45′13.5″W, *D. S. Barrington 1283* (GH, VT).

Polystichum speciosissimum (A. Braun ex Kunze) R. M. Tryon & A. F. Tryon × **P. talamancanum** Barrington

Documented twice (Barrington, 1990), this hybrid, from above treeline on the Cerro de la Muerte, combines the greater pinnule dissection of *Polystichum speciosissimum* with the strongly spinulose pinnule margins of *P. talamancanum*. Petiole scale hue is intermediate between the progenitors, and pinna-rachis scale hue is pale, favoring *P. speciosissimum*. The heritage of the cited specimens was documented with cytological and isozyme work (Barrington, 1990).

Specimens examined. COSTA RICA. **San José:** SE slope of highest peak of Cerro de la Muerte, *D. S. Barrington 973* (VT); Cerro de la Muerte, S side of N summit with radio towers, *D. S. Barrington 1500* (VT).

Species Excluded from Costa Rica

Polystichum aculeatum (L.) Roth, Tent. Fl. Germ. 3(1): 79. 1799. Basionym: *Polypodium aculeatum* L., Sp. Pl. 2: 1090. 1753. TYPE: "Habitat in Europa" (lectotype, designated by Alston [1940: 164], *A. van Royen s.n.*, L [Herb. L.B. 908.311–72] not seen).

The name *Polystichum aculeatum* was applied by Carl Christensen (Christensen, 1905–1906) to a broad array of twice-pinnate *Polystichum* species from throughout the world, which he reduced to varietal status. However, *P. aculeatum* is currently construed as an allotetraploid species confined to Europe (Tutin et al., 1993). It combines the features of its diploid progenitors *P. lonchitis* and *P. setiferum* (Forssk.) Moore ex Woynar; none of these plants grows in tropical America.

Polystichum fournieri A. R. Sm., Amer. Fern J. 70: 27. 1980. Replaced name: *Polystichum muelleri* Mett. ex E. Fourn. Mexic. Pl. 1: 91.1872, non *Polystichum muelleri* Schumach., 1803. TYPE: Mexico. Chiapas: forêts des pins, *J. J. Linden s.n.* (lectotype, designated by A. R. Smith [1980: 27], P!).

This name has been applied to an array of small polystichums from high elevations in Costa Rica. These plants are mostly *Polystichum lilianiae* and *P. turrialbae*. *Polystichum fournieri* is endemic to northern Central America and Mexico (Barrington, 2003).

Polystichium lehmannii Hieron., Bot. Jahrb. Syst. 34: 452. 1904. TYPE: Colombia. Depto. Cauca: near Los Motilones, Mt. Sotará, 3000 m, *F. C. Lehmann 3674* (holotype, B!; isotype, US!).

This name applies to plants from Andean South America.

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REVISION OF THE NORTH AMERICAN SPECIES OF *GRINDELIA* (ASTERACEAE)[1]

Adriana Bartoli[2] *and Roberto D. Tortosa*[3]

Abstract

A revision of North American species of the genus *Grindelia* Willd. (Asteraceae) was carried out. Forty-one species, 10 varieties, and two forms are recognized, and a key is given. The following new combinations are made: *G. fastigiata* Greene var. *revoluta* (Steyerm.) Adr. Bartoli & Tortosa [≡ *G. revoluta* Steyerm.], *G. hirtella* (B. L. Rob. & Greenm.) Adr. Bartoli & Tortosa [≡ *G. squarrosa* (Pursh) Dunal var. *hirtella* B. L. Rob. & Greenm.], *G. humilis* Hook. & Arn. var. *platyphylla* (Greene) Adr. Bartoli & Tortosa [≡ *G. robusta* Nutt. var. *platyphylla* Greene], *G. lanceolata* Nutt. var. *subincisa* (Greene) Adr. Bartoli & Tortosa [≡ *G. subincisa* Greene], *G. leptocarpa* (De Jong & Beaman) Adr. Bartoli & Tortosa [≡ *Olivaea leptocarpa* De Jong & Beaman], *G. squarrosa* f. *pseudopinnatifida* (D. Löve & J.-P. Bernard) Adr. Bartoli & Tortosa [≡ *G. perennis* A. Nelson f. *pseudopinnatifida* D. Löve & J.-P. Bernard], *G. squarrosa* var. *eligulata* (Steyerm.) Adr. Bartoli & Tortosa [≡ *G. oxylepis* Greene var. *eligulata* Steyerm.], and *G. tricuspis* (Sch. Bip.) Adr. Bartoli & Tortosa [≡ *O. tricuspis* Sch. Bip.]. *Aster glutinosus* Cav. is proposed as lectotype for the genus *Demetria* Lag. and a neotype is designated for *D. spathulata* Lag. The following names are lectotypified: *G. inuloides* Willd., *G. lanceolata*, *G. nana* Nutt., *G. nana* var. *integrifolia* Nutt., *G. platylepis* Greene, *G. subincisa* [≡ *G. lanceolata* var. *subincisa*], and *G. texana* Scheele [≡ *G. lanceolata* var. *texana* (Scheele) Shinners]. Seventeen taxa are illustrated for the first time.

Resumen

Se lleva a cabo una revisión de las especies norteamericanas del género *Grindelia* Willd. (Asteraceae). Se reconocen 41 especies, 10 variedades y dos formas y se incluye una clave para su determinación. Se realizan las siguientes nuevos combinaciones: *G. fastigiata* Greene var. *revoluta* (Steyerm.) Adr. Bartoli & Tortosa [≡ *G. revoluta* Steyerm.], *G. hirtella* (B. L. Rob. & Greenm.) Adr. Bartoli & Tortosa [≡ *G. squarrosa* (Pursh) Dunal var. *hirtella* B. L. Rob. & Greenm.], *G. humilis* Hook. & Arn. var. *platyphylla* (Greene) Adr. Bartoli & Tortosa [≡ *G. robusta* Nutt. var. *platyphylla* Greene], *G. lanceolata* Nutt. var. *subincisa* (Greene) Adr. Bartoli & Tortosa [≡ *G. subincisa* Greene], *G. leptocarpa* (De Jong & Beaman) Adr. Bartoli & Tortosa [≡ *Olivaea leptocarpa* De Jong & Beaman], *G. squarrosa* f. *pseudopinnatifida* (D. Löve & J.-P. Bernard) Adr. Bartoli & Tortosa [≡ *G. perennis* A. Nelson f. *pseudopinnatifida* D. Löve & J.-P. Bernard], *G. squarrosa* var. *eligulata* (Steyerm.) Adr. Bartoli & Tortosa [≡ *G. oxylepis* Greene var. *eligulata* Steyerm.] y *G. tricuspis* (Sch. Bip.) Adr. Bartoli & Tortosa [≡ *O. tricuspis* Sch. Bip.]. Se propone *Aster glutinosus* Cav. como lectotipo del género *Demetria* Lag. y se designa un neotipo para *D. spathulata* Lag. Los siguientes nombres son lectotipificados: *G. inuloides* Willd., *G. lanceolata*, *G. nana* Nutt., *G. nana* var. *integrifolia* Nutt., *G. platylepis* Greene, *G. subincisa* [≡ *G. lanceolata* var. *subincisa*] y *G. texana* Scheele [≡ *G. lanceolata* var. *texana* (Scheele) Shinners]. Se ilustran por primera vez 17 taxa.

Key words: Asteraceae, *Grindelia*, North America.

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This paper treats the species of *Grindelia* Willd. of North America. *Grindelia* is a New World genus of Asteraceae and a member of the tribe Astereae, subtribe Solidagininae, with a disjunct distribution in North America and austral South America. In South America, the genus occurs in Peru, Chile, Bolivia, Brazil, Argentina, and Uruguay, and has been taxonomically treated by Cabrera (1931), Bartoli and Tortosa (1999, 2003), and Granda Paucar et al. (2000). The boreal species of *Grindelia* that inhabit Canada, the United States, and Mexico were monographed by Steyermark (1934), who recognized 45 species, 40 varieties, and 25 forms. Subsequently, partial treatments have been done by Reveal and Beatley (1971), Nesom (1990, 1992), Lane (1992, 1993), and Strother and Wetter (2006), who introduced new taxa, nomenclatural changes, and new taxonomic interpretations. Further, Nesom has made available to the authors his unpublished manuscript for Mexican *Grindelia*. Nesom et al. (1993) included the monotypic genus *Prionopsis* Nutt. within *Grindelia*, which was followed by Strother and Wetter (2006) but not by Lane and Hartman (1996).

We agree with Lane and Hartman (1996) that *Prionopsis* is a different genus from *Grindelia* because of its pappus with persistent awns, absence of glands on the abaxial surface of phyllaries, and costate achenes.

Lane (1992, 1993) hypothesized the existence of hybrids between different species of *Grindelia*, but no research was done to prove this assumption.

Taxonomic Treatment

Grindelia Willd., Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 1: 259. 1807. TYPE: *Grindelia inuloides* Willd.

Donia R. Br., Hortus Kew. (W. T. Aiton), ed. 2, 5: 82. 1813, non *Donia* G. Don & D. Don ex G. Don, 1832 (Fabaceae). *Doniana* Raf., Amer. Monthly Mag. & Crit. Rev. 2: 268. 1818, nom. illeg. superfl. TYPE: *Aster glutinosus* Cav. [≡ *Donia glutinosa* (Cav.) R. Br.].

Aurelia Cass., Bull. Sci. Soc. Philom. Paris, 175. 1815, nom. illeg. superfl. TYPE: *Aster glutinosus* Cav. [≡ *Aurelia glutinosa* (Cav.) Cass.].

Demetria Lag., Gen. Sp. Pl. [Lagasca]: 30. 1816, nom. illeg. superfl. (lectotype, designated here, *Aster glutinosus* Cav. [≡ *Demetria glutinosa* (Cav.) Lag.]).

Hoorebekia Cornel., Hort. Gand. 13–14. 1817. TYPE: *Hoorebekia chiloensis* Cornel. [= *Grindelia chiloensis* (Cornel.) Cabrera].

Olivaea Sch. Bip. ex Benth., Hooker's Icon. Pl. 12: 2–3, tab. 1103. 1876. TYPE: *Olivaea tricuspis* Sch. Bip. [≡ *Grindelia tricuspis* (Sch. Bip.) Adr. Bartoli & Tortosa].

Golionema S. Watson, Bot. Gaz. 16: 267. 1891. Replaced name: *Oligonema* S. Watson, Proc. Amer. Acad. Arts 26: 138. 1891, nom. illeg. superfl., non *Oligonema* Rostaf., Monogr., 291. 1875 (Myxomycete, Trichiaceae). TYPE: *Golionema heterophyllum* (S. Watson) S. Watson (epithet ending corrected by S. Watson, 1891, to neuter ending, cf. Art. 62.2c.). [≡ *Grindelia tricuspis* (Sch. Bip.) Adr. Bartoli & Tortosa].

Annual or perennial, herbs, subshrubs, or shrubs; indumentum of simple hairs, stipitate glandular trichomes, and/or sessile glandular trichomes on stems, leaves, and phyllaries. Leaves alternate, sessile or petiolate, entire to pinnatisect, margin entire to toothed, teeth blunt or ending in a group of sessile glandular trichomes or in a sclerotic tip, sometimes spinulose. Heads solitary or grouped, radiate or discoid; involucre hemispheric or hemispheric-campanulate; phyllaries in 4 to 8 series, subequal to abruptly graduated, free or ± connate, usually with a sclerified portion; receptacle pitted, epaleate, glabrous. Ray florets pistillate, corolla yellow, entire, lobed or toothed; tube usually glabrous, rarely stipitate glandular trichomes; style with branches linear-elliptic, apex obtuse, glabrous. Disk florets perfect, tubular, limb 5-toothed; tube usually glabrous, rarely stipitate glandular trichomes; anthers shortly sagittate at the base, apex of connective ovate to ovate-elliptic; style branches in disk florets flattened, elliptic, acute, with sweeping papillose trichomes on the outer side. Achenes flattened or prismatic, sometimes winged, glabrous; pappus 2 to 5 scales or setiform awns, or 2 to 80 bristles, white, deciduous. Chromosome number: $x = 6$ (Whitaker & Steyermark, 1935: 71; Powell & Turner, 1963: 130).

Discussion. When Lagasca (1816) described *Demetria* as a new genus, he included two species, *D. spathulata* Lag. from Mexico, and *D. glutinosa*, a South American species. We choose *D. glutinosa* as lectotype for the genus, for which there is a type and a plate (Cavanilles, 1793: pl. 168) available.

Several of the genus-level synonyms for *Grindelia* are typified by *Aster glutinosus*, a species from Peru (cf. Cavanilles, 1798; McVaugh, 2000: 137).

Aster glutinosus Cav., Icon. 2(2): 53–54, tab. 168. 1793. *Donia glutinosa* (Cav.) R. Br., Hortus Kew. (W. T. Aiton), ed. 2, 5: 82. 1813. *Grindelia glutinosa* (Cav.) Mart., Pl. Hort. Acad. Erlang., 182. 1814. *Aurelia glutinosa* (Cav.) Cass., Bull. Sci. Soc. Philom. Paris, 175. 1815. *Demetria glutinosa* (Cav.) Lag., Gen. Sp. Pl. [Lagasca], 30. 1816. *Grindelia glutinosa* (Cav.) Dunal, Mém. Mus. Hist. Nat. 5: 49. 1819, nom. illeg. superfl. TYPE: "Mexico" [flowered at the Royal Botanical Garden of Madrid in December (1792 or earlier)], "Aster glutinosus sp. nov.," s.d., *s. coll.*

s.n. (lectotype, designated here, US-00145634 ex BM digital image!).

Cavanilles's type was not found at MA, but there is a specimen at US annotated from Mexico, as *s. coll.*, "Aster glutinosus sp. nov." (US-00145634 ex BM) that was annotated by Steyermark (1 Mar. 1933) as "part of type collection of *Aster glutinosus* Cav.," and that fits the protologue. We designate this specimen here as lectotype of *A. glutinosus*.

Diagnostic Characters for the North American Species of *Grindelia*

Grindelia consists of annual plants with subligneous floriferous stems such as *G. adenodonta* (Steyerm.) G. L. Nesom (*Palmer 10134*, MO), *G. confusa* Steyerm. (*Correll & Johnston 20165*, TEX), and *G. grandiflora* Hook. (*Cory 52450*, PH), or of perennial plants with floriferous stems that arise from a rhizome (*G. greenmanii* Steyerm., *Mueller 2173*, MO; *G. leptocarpa* (De Jong & Beaman) Adr. Bartoli & Tortosa, *Worthington 8963*, NY; *G. obovatifolia* S. F. Blake, *Nesom & Morgan 6789*, MO), a lignotuber (*G. turneri* G. L. Nesom, *Hinton 22268*, TEX), or a rosette of leaves (*G. camporum* Greene, *Howell 10827*, MO) that originates proleptically from renewals at the base of stems from the previous year. Two aquatic taxa, *G. leptocarpa* and *G. tricuspis*, have noteworthy fistulose stems.

Leaves in *Grindelia* may be succulent, subcoriaceous, or herbaceous; sessile or with blades that are attenuate into the pseudopetiole; entire, lobed, or pinnatisect. The blades may range from linear, elliptic, oblong, ovate, obovate, spatulate, to somewhat triangular, or fiddle-shaped. Blade bases may be cuneate, cordate, or clasping, and sometimes auriculate; blade apices may be acute, acuminate, rounded, obtuse, or mucronate. Leaf margins may be crenate, denticulate, serrate, toothed, and sometimes scabrous. Marginal teeth (Fig. 1) may be dull, ending in a group of sessile glandular trichomes, as in *G. adenodonta* (*Wetter 605*, NY), *G. squarrosa* (Pursh) Dunal (*Engelmann 650*, MO), and *G. turneri* (*Hinton 22268*, TEX), or in a sclerotic tip as in *G. arizonica* A. Gray (*Baker 682*, GH) and *G. camporum* (*Howell 10827*, MO), or in a spinule as in *G. lanceolata* Nutt. (*Bush 220*, MO).

Heads in *Grindelia* may be radiate or discoid, solitary, and sessile to pedunculate. The involucre may be hemispheric to urceolate or campanulate, and sometimes broadly urceolate or obconic. Phyllaries are disposed in four to eight series, subequal or graduated; filiform, linear, elliptic, ovate, or obovate, subulate (gradually tapering to the apex) or acuminate (tapering to the apex into a narrow or slender point), with the margin entire or scabrous; erect, spreading, curved, revolute, or reflexed. The phyllary base is usually sclerified; when subulate the apex may be acute, mucronate, or spinulose, terete to flattened, with straight to curved tips; when acuminate, the acumen may be shorter than, equal to, or longer than the base, filiform, linear, triangular, or ovate, flattened to terete, erect to reflexed.

Indumentum in *Grindelia* includes simple hairs, stipitate glandular trichomes, and sessile glandular trichomes that occur frequently in pits.

Ray florets in *Grindelia* range from 12 to 60 per head, with the corolla tube glabrous or with stipitate glandular trichomes. The ray ligule may be narrowly linear to elliptic, oblong or ovate, with the apex entire, lobed, or toothed. Disk florets are numerous, and the corolla may have a gradually or abruptly ampliate throat.

Achenes in *Grindelia* may be yellowish to dull brown, light brown to stramineous or dark brown, 2- to 4-angled, prismatic or flattened, elliptic to globose or subquadrate to quadrate, sometimes obconic, and occasionally winged. The achene surface may be smooth, rugose, striate, barely tuberculate to tuberculate, or with deep furrows or shallow incisions, with the achene apex rounded, truncate, with one or two teeth or knobby, or forming a crown. The pappus is caducous and varies from two to five subulate scales (greatest width ca. three times the radial thickness) to setiform awns (greatest width ca. two times the radial thickness), or bristles (width about equal to radial thickness) that are smooth to barbellate (sensu Strother & Wetter, 2006).

Gametophytic chromosome numbers have been consistently reported as $n = 6$: Chambers et al., 1998 (*Grindelia integrifolia* DC.); De Jong and Beaman, 1963 (*G. leptocarpa* and *G. tricuspis*); Dunford, 1986 (*G. arizonica*, *G. camporum*, *G. fastigiata* Greene var. *fastigiata*, *G. fastigiata* var. *revoluta* (Steyerm.) Adr. Bartoli & Tortosa, *G. grandiflora*, *G. havardii* Steyerm., *G. lanceolata* var. *lanceolata*, *G. lanceolata* var. *texana* (Scheele) Shinners, *G. nana* Nutt. var. *nana*, and *G. subalpina* Greene); Lane and Li, 1993 (*G. camporum*, *G. confusa*, *G. hallii* Steyerm., and *G. squarrosa*); Pinkava and Keil, 1977 (*G. arizonica*, *G. grandiflora*, *G. greenmanii*, and *G. squarrosa* f. *squarrosa*); Powell and Turner, 1963 (*G. inuloides*, *G. pusilla* (Steyerm.) G. L. Nesom, and *G. robinsonii* Steyerm.); Raven et al., 1960 (*G. hallii*); Semple et al., 1989 (*G. inuloides*). Sporophytic chromosome counts have been reported as $2n = 12$: Cronquist, 1994 (*G. fastigiata*, *G. laciniata* Rydb., *G. nana*, *G.*

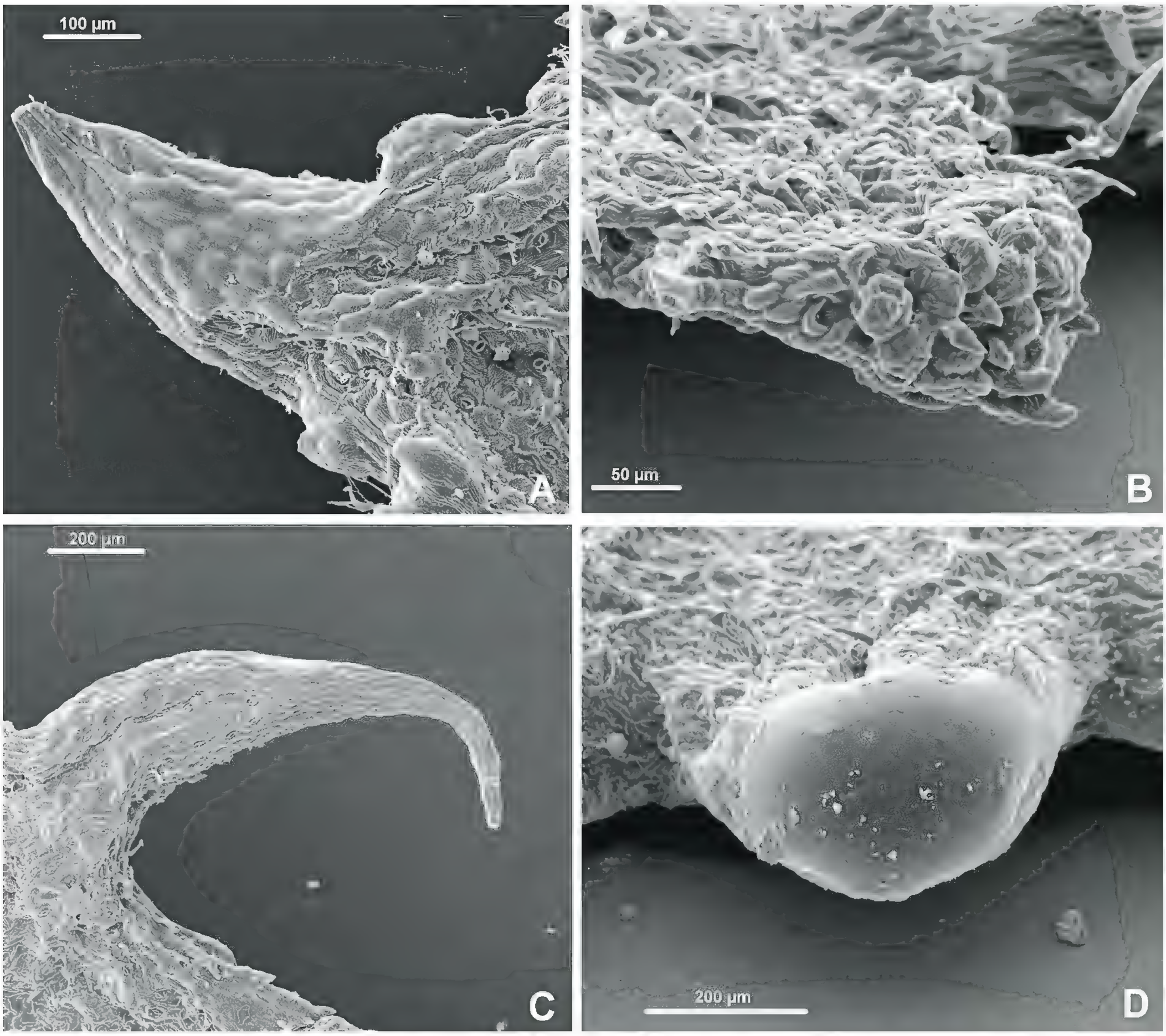

Figure 1. Marginal teeth of the leaves of *Grindelia* Willd. —A. Leaf tooth ending in a sclerotic tip. Micrograph from *G. camporum* Greene, *M. A. Lane 3098* (PH). —B. Leaf tooth ending in a group of sessile glandular trichomes. Micrograph from *G. turneri* G. L. Nesom, *G. B. Hinton 17760* (TEX). —C. Leaf tooth ending in a spinule. Micrograph from *G. lanceolata* Nutt., *M. A. Wetter 485* (SI). —D. Micrograph corresponds to B, but the tooth surface is covered by resins secreted by the glandular trichomes.

nana var. *discoidea* (Nutt.) A. Gray, and *G. squarrosa*); Dunford, 1964 (*G. camporum*); Dunford, 1969 (*G. grandiflora*, *G. lanceolata* var. *texana*, *G. microcephala* DC., and *G. oolepis* S. F. Blake); Lane, 1993 (*G. hirsutula* Hook. & Arn. and *G. humilis* Hook. & Arn.); Lane and Li, 1993 (*G. humilis*); McLaughlin, 1986 (*G. camporum*); Morton, 1981 (*G. nana* and *G. squarrosa*); Pinkava and Keil, 1977 (*G. grandiflora* and *G. humilis*); Powell and Turner, 1963 (*G. oxylepis* Greene, *G. oxylepis* var. *eligulata* Steyerm., and *G. squarrosa* var. *eligulata* (Steyerm.) Adr. Bartoli & Tortosa); Powell and Powell, 1978 (*G. havardii*); Pinkava and Keil, 1977 (*G. squarrosa* var. *eligulata* and *G. squarrosa* var. *nuda* (Alph. Wood) A. Gray); Raven et al., 1960 (*G. hallii*, *G. hirsutula*, *G. humilis*, *G. squarrosa*, and *G. squarrosa* var. *nuda*); Semple et al., 1989 (*G. humilis* and *G. oxylepis*); Semple et al., 1992 (*G. camporum*); Whitaker and Steyermark, 1935 (*G. camporum*, *G. columbiana* (Piper) Rydb., *G. decumbens* Greene, *G. lanceolata*, *G. nana*, and *G. perennis* A. Nelson); Zhao, 1996 (*G. obovatifolia* and *G. tenella* Steyerm.); Zhao and Turner, 1993 (*G. grandiflora* and *G. pusilla*). Mitotic chromosome counts also include $2n = 24$: Dunford, 1964 (*G. camporum*, *G. hirsutula*, and *G. stricta* DC.); Dunford, 1969 (*G. lanceolata*); Lane, 1993 (*G. fraxinipratensis* Reveal & Beatley, *G. humilis*, and *G. humilis* var. *platyphylla* (Greene) Adr. Bartoli & Tortosa); McLaughlin, 1986 (*G. camporum*); Morton, 1981 (*G. integrifolia*); Semple et al., 1989 (*G. subdecurrens* DC.); Whitaker and Steyermark, 1935 (*G. camporum*, *G. hirsutula* var. *brevisquama*

Steyerm., *G. humilis*, *G. maritima* (Greene) Steyerm., *G. rubricaulis* DC. var. *elata* Steyerm., *G. rubricaulis* var. *platyphylla* (Greene) Steyerm., and *G. squarrosa* var. *nuda*).

Taxonomic Key to North American Species of *Grindelia*

1a. Aquatic plants; stems fistulose 2
1b. Terrestrial plants; stems not fistulose 3
2a. Stems 1 or 2, scarcely ramified; heads 2–3 cm diam.; involucre 4–7 × 10–15 mm; achenes 2-angled; pappus 2 to 5 bristles ..... 20. *G. leptocarpa*
2b. Stems several, ramified; heads 3–4 cm diam.; involucre 10–15 × 15–20 mm; achenes 2- or 3-winged; pappus 5 to 12 bristles ..... 39. *G. tricuspis*
3a. Phyllaries in subequal series 4
3b. Phyllaries in graduated or strongly graduated series 15
4a. Phyllaries subulate 5
4b. Phyllaries acuminate 8
5a. Perennial subshrubs with xylopodium; stems prostrate ..... 12. *G. hintoniorum*
5b. Annual subshrubs; stems erect 6
6a. Plants 0.08–0.15 m; achenes sharply cut with transverse furrows ..... 31. *G. pusilla*
6b. Plants 0.25–1.3 m; achenes smooth, rugose, or striate 7
7a. Leaves with sessile glandular trichomes, not in pits, and stipitate trichomes; achenes obconic, the inner flattened; pappus of 2 subulate scales ..... 1. *G. adenodonta*
7b. Leaves with sessile glandular trichomes in pits; achenes globose; pappus of 2 or 3 setiform awns ..... 22. *G. microcephala*
8a. Leaves with teeth ending in a sclerotic tip or a curved spinule 9
8b. Leaves with teeth ending in a group of sessile glandular trichomes 13
9a. Teeth ending in a curved spinule ..... 19. *G. lanceolata*
9b. Teeth ending in a sclerotic tip 10
10a. Phyllaries with margin scabrous; acumen filiform, terete or subterete ..... 33. *G. scabra*
10b. Phyllaries with margin entire; acumen linear, triangular, elliptic, or narrowly ovate, flat or subterete 11
11a. Phyllary acumen linear-elliptic to narrowly ovate; pappus of 2 bristles ..... 17. *G. inuloides*
11b. Phyllary acumen triangular 12
12a. Plants rhizomatous; acumen shorter than the base; pappus of 2 or 3 bristles ..... 9. *G. greenmanii*
12b. Plants not rhizomatous; acumen as long as the base; pappus of 2 to 5 curved, subulate scales ..... 15. *G. humilis*
13a. Plants with xylopodium; stems prostrate with tips rising upward, not or few ramified; heads 1.4–2 cm diam.; pappus of 2 setiform awns ..... 40. *G. turneri*
13b. Plants without xylopodium; stems ascendent or erect, ramified; heads 3–5 cm diam.; pappus of 2 or 3 bristles ... 14
14a. Outer phyllaries with acumen very long and narrow; achenes subquadrate, smooth or longitudinally striate with shallow transverse incisions at apex ..... 24. *G. nelsonii*
14b. Outer phyllaries with acumen equal to or shorter than base; achenes elliptic, 2- or 3-angled, smooth or slightly rugose ..... 29. *G. palmeri*
15a. Phyllaries acuminate 16
15b. Phyllaries subulate 36
16a. Leaves with sessile glandular trichomes in pits 17
16b. Leaves with sessile glandular trichomes not in pits 23
17a. Leaves with teeth ending in a group of glandular trichomes 18
17b. Leaves with teeth ending in a sclerotic tip 19
18a. Achenes smooth, rugose, or slightly furrowed; pappus of 2 or 3 curved, setiform awns ..... 34. *G. squarrosa*
18b. Achenes with prominent longitudinal furrows; pappus of 2 to 4 straight bristles ..... 36. *G. subdecurrens*
19a. Acumen of phyllaries revolute; heads radiate or discoid 20
19b. Acumen of phyllaries erect or curved, not reflexed or revolute; heads radiate 21
20a. Heads pedunculate; involucre 7–10 × 7–10 mm; stems several, somewhat decumbent at the base ... 23. *G. nana*
20b. Heads sessile or subsessile; involucre 10–14 × 9–17 mm; stems 2 to 4, erect ..... 6. *G. fastigiata*
21a. Heads 0.8–1.4 cm diam.; phyllaries with acumen triangular, flat, erect; achenes with a truncate to knobby apex; pappus of 2 bristles ..... 7. *G. fraxinipratensis*
21b. Heads 1.5–3 cm diam. 22
22a. Heads 2–3 cm diam.; phyllaries with acumen terete or subterete, curved; achenes with a crown at the apex; pappus of 2 or 3 subulate scales ..... 3. *G. camporum*
22b. Heads 1.5–2 cm diam.; phyllaries with acumen triangular, subterete, erect; achenes with apex truncate; pappus of 2 to 5 setiform awns ..... 5. *G. decumbens*
23a. Stipitate glandular trichomes absent 24
23b. Stipitate glandular trichomes present 30
24a. Stems prostrate with tips rising upward; heads subsessile ..... 21. *G. macvaughii*
24b. Stems erect; heads pedunculate 25
25a. Rhizomatous, perennial plants ..... 32. *G. robinsonii*
25b. Not rhizomatous, annual, biannual, or perennial plants 26
26a. Heads 1.5–2 cm diam 27

26b. Heads 2–3.8 cm diam 28
27a. Phyllaries spreading or reflexed, with acumen subterete or terete; stems hairy; achenes subquadrate, tuberculate, apex truncate ..... 14. *G. hirtella*
27b. Phyllaries erect, with acumen flat; stems glabrous; achenes elliptic, 4-angled, striate, with a crown at the apex ..... 2. *G. arizonica*
28a. Perennial plants with xylopodium; acumen reflexed or revolute; pappus of 2 to 8 setiform awns .. 35. *G. subalpina*
28b. Annual plants without xylopodium; acumen erect to spreading; pappus of 2 or 3 bristles 29
29a. Leaves with simple hairs absent; acumen of the phyllaries filiform; achenes monomorphic, broadly elliptic, 2- or 3-angled, longitudinally striate or furrowed, apex knobby or forming a crown ..... 8. *G. grandiflora*
29b. Leaves with simple hairs present; acumen of the phyllaries not filiform; achenes dimorphic, subquadrate, strongly furrowed to tuberculate, the innermost flattened with longitudinal superficial nerves, apex truncate ..... 38. *G. tenella*
30a. Leaves pinnatisect; plants ca. 0.15 m ..... 4. *G. confusa*
30b. Leaves not pinnatisect; plants higher than 0.15 m 31
31a. Leaves clasping or auriculate 32
31b. Leaves not clasping nor auriculate 34
32a. Heads pedunculate, 2.5 cm diam.; leaves with stipitate glandular trichomes along the middle nerve, teeth ending in a group of sessile glandular trichomes ..... 11. *G. havardii*
32b. Heads sessile; leaves with stipitate glandular trichomes on both blade surfaces 33
33a. Heads 2.5–3 cm diam.; leaves with apex acute or acuminate, teeth ending in a sclerotic tip; phyllaries with acumen filiform ..... 16. *G. integrifolia*
33b. Heads 1.6–2 cm diam.; leaves with apex obtuse, teeth blunt; phyllaries with acumen flat to subterete ..... 25. *G. oaxacana*
34a. Rhizomatous herbs; basal leaves with blades attenuate into a pseudopetiole as long as the blade ..... 26. *G. obovatifolia*
34b. Not rhizomatous subshrubs or shrubs; leaves all sessile 35
35a. Heads 1–1.5 cm diam.; achenes subquadrate with transverse and sometimes longitudinal furrows; pappus of 4 bristles ..... 37. *G. sublanuginosa*
35b. Heads 2.5–3 cm diam.; achenes elliptic, rugose or striated; pappus of 2 to 5 setiform awns .... 30. *G. paysonorum*
36a. Leaves with sessile glandular trichomes in pits 37
36b. Leaves with sessile glandular trichomes not in pits 39
37a. Basal and middle cauline leaves pinnatisect; heads 1 cm diam ..... 18. *G. laciniata*
37b. Leaves not pinnatisect; heads 1.5–2 cm diam 38
38a. Leaves narrowly elliptic; involucre hemispheric to hemispheric-campanulate; pappus of 2 bristles; achenes smooth to furrowed ..... 10. *G. hallii*
38b. Leaves oblong or obovate; involucre urceolate; pappus of 2 or 3 setiform awns; achenes tuberculate ..... 28. *G. oxylepis*
39a. Heads discoid; rhizomatous perennial herbs ..... 27. *G. oolepis*
39b. Heads radiate; not rhizomatous perennial subshrubs 40
40a. Heads 1.3–1.5 cm diam.; leaves with minutely stipitate glandular trichomes; achenes barely tuberculate; pappus of 2 setiform awns ..... 41. *G. villarrealii*
40b. Heads 3.5–4 cm diam.; leaves with sessile glandular trichomes; achenes smooth or striate; pappus of 2 to 4 subulate scales ..... 13. *G. hirsutula*

1. Grindelia adenodonta (Steyerm.) G. L. Nesom, Phytologia 73: 327. 1992. Basionym: *Grindelia microcephala* DC. var. *adenodonta* Steyerm., Ann. Missouri Bot. Gard. 21: 467. 1934. TYPE: U.S.A. Texas: 39 mi. W of San Felipe, July–Aug. 1844, *F. Lindheimer 255* (holotype, MO-130145!; isotypes, GH [barcode] 00008432!, PH [barcode] 00047861!, US [barcode] 00127642!). Figure 2.

Grindelia microcephala DC. f. *angustior* Steyerm., Ann. Missouri Bot. Gard. 21: 469. 1934, syn. nov. [described under *Grindelia microcephala* var. *adenodonta*]. TYPE: U.S.A. Texas: Uvalde Co., near Uvalde, 28 Apr. 1928, *E. J. Palmer 33590* (holotype, MO-945114!; isotypes, LL [barcode] 00373594 digital image!, NY [barcode] 00169616!).

Annual subshrubs, 0.3–1.3 m; stem 1, erect, ramified, hirsute or villous, sometimes lanuginous at the apex. Leaves sessile, ovate, triangular-ovate, elliptic, or obovate, clasping; blade apex obtuse to acute, margin with rounded teeth ending in a group of sessile glandular trichomes, simple hairs, and often also sessile and stipitate glandular trichomes, on both blade surfaces; basal leaves 4.5–9 × 1.5–3 cm; cauline leaves auriculate, 2–5.5 × 0.6–2.5 cm. Heads radiate, sessile or subsessile, 0.8–1.5 cm diam.; involucre hemispheric, resinous, 8–12 × 10–12 mm; phyllaries in 4 to 6 subequal series, subulate, subcoriaceous, with sessile glandular trichomes at the apex; the outer and middle bracts narrowly ovate, 8–10 mm, erect to spreading, with a flattened, straight to curved tip, 3–5 mm; the upper phyllary narrowly elliptic, 12 mm, erect. Ray florets 20 to 28; tube glabrous, ligule elliptic or ovate, 8–12 mm, apex entire or toothed. Disk florets with corolla 6–7 mm, with a gradually ampliate throat. Achenes yellowish

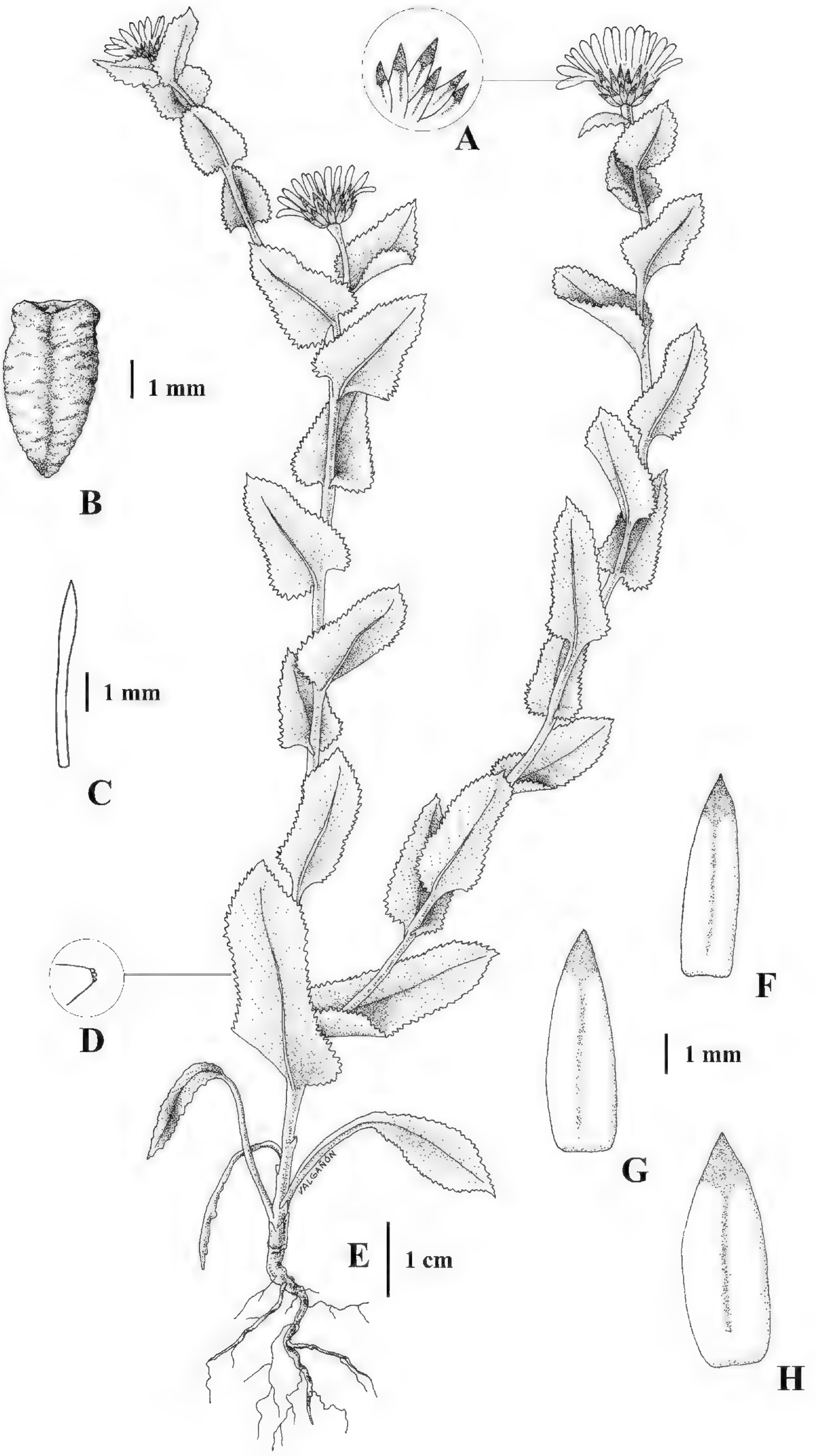

Figure 2. *Grindelia adenodonta* (Steyerm.) G. L. Nesom. —A. Part of the involucre, inner phyllary series represented. —B. Achene, 2- or 3-angled, showing the rugose or striate surface. —C. Pappus, one of the two subulate scales. —D. Leaf tooth, with rounded apex, ending in a group of sessile, glandular trichomes. —E. Fertile habit. F–H. Representative phyllaries. —F. Outer series. —G. Middle series. —H. Inner series. Drawn from *A. Ruth 284* (PH).

or dull brown, obconic, 2- or 3-angled, the inner achenes flattened, 3–4.5 mm, rugose or striate, apices with a crown; pappus of 2 subulate scales, apex dilated, 5–6 mm, straight or somewhat curved, smooth. Chromosome number not known.

Distribution and habitat. *Grindelia adenodonta* has been collected from thickets, prairies, and along streams, from 10 to 200 m in Texas (U.S.A.).

Phenology. *Grindelia adenodonta* flowers from June to October.

Etymology. The specific epithet is taken from the Greek "adeno-," meaning "gland" and "-odonto," meaning "tooth," which refers to the marginal teeth of the leaves that end in a group of sessile, glandular trichomes, a characteristic also seen elsewhere for other species in the genus.

Common name. Lone-star gumweed (<http://plants.usda.gov/>).

Discussion. Among the annual species, *Grindelia adenodonta* is characterized by its small radiate heads with subulate phyllaries in subequal series. Similar to *G. microcephala* and *G. pusilla*, with similar radiate heads not exceeding 1.5 cm and phyllaries, this taxon is also from Texas. *Grindelia adenodonta* is recognized by its rugose or striate achenes, the inner flattened, with two subulate scales to 6 mm, in contrast to the smoother, globose or obconic achenes topped by two or three setiform awns seen in *G. microcephala* and *G. pusilla*. In *G. microcephala* f. *angustior*, the achenes resemble those of *G. adenodonta*.

Additional specimens examined. U.S.A. **Texas:** Bexar Co., San Antonio, *Mr. & Mrs. J. Clemens 948* (MO); Comanche Spring, New Braunfels, *F. Lindheimer 919* (NY); Denton Co., Post Oak Belt, ca. 8 mi. S of Denton on Hickory Creek, old Alton Rd., *E. Whitehouse 16425* (NY); Jackson Co., along TX 35 just N of Port Comfort, *M. A. Wetter 605* (NY); Nueces Co., Corpus Christi, *A. A. Heller 1820* (PH); Uvalde Co., Sabinal, *E. J. Palmer 10134* (MO); Tarrant Co., Trinity River, *A. Ruth 284* (PH).

2. Grindelia arizonica A. Gray, Proc. Amer. Acad. Arts 17: 208. 1882, as "Arizonica." TYPE: U.S.A. Arizona: mesa of Black River, 550 ft., Sep. 1874, *J. T. Rothrock 796* (holotype, GH [barcode] 00008420!; isotypes, GH [barcode] 00008422!, US [barcode] 00127632 digital image!).

Grindelia setulifera Wooton & Standl., Contr. U.S. Natl. Herb. 16: 179. 1913. TYPE: U.S.A. New Mexico: high summits, Mogollon Mtns., Sep. 1881, *H. H. Rusby 206* (holotype, US 00127658 [barcode] digital image!; isotypes, F [barcode] 0050292F digital image!, MICH [barcode] 1107424 digital image!, MO [barcode] 714107!, NY [barcode] 169626!).

Grindelia arizonica A. Gray var. *dentata* Steyerm., Ann. Missouri Bot. Gard. 21: 508. 1934. TYPE: U.S.A. New Mexico: Grant Co., Bear Mtn., near Silver City, ca. 8000 ft., 19 Sep. 1903, *O. B. Metcalfe 744* (holotype, US [barcode] 00127633 digital image!; isotypes, MO [barcode] 714106!, NY [barcode] 169597!, RM [barcode] 0001115 digital image!).

Grindelia arizonica A. Gray var. *microphylla* Steyerm., Ann. Missouri Bot. Gard. 21: 508. 1934. TYPE: U.S.A. Arizona: Greenlee Co., along San Francisco River, 10 mi. N of Clifton, 7 Sep. 1902, *A. Davidson 736* (holotype, GH [barcode] 00008424!).

Grindelia arizonica A. Gray var. *stenophylla* Steyerm. Ann. Missouri Bot. Gard. 21: 507. 1934. TYPE: U.S.A. Colorado: near Bayfield, 12 Aug. 1904, *E. O. Wooton 2568* (holotype, US [barcode] 00127634 digital image!).

Perennial subshrubs, 0.25–0.7 m, sometimes with conspicuous xylopodium; stem 1, erect, ramified, glabrous. Leaves sessile, coriaceous, oblong-spatulate to elliptic; blade apex acute, mucronate, margin toothed, teeth ending in a sclerotic tip, simple hairs absent or only at the margins, sessile glandular trichomes on both blade surfaces; basal leaves 5.5–6 × 1–1.1 cm, blades attenuate into a pseudopetiole; cauline leaves 1.5–4.5 × 0.6–1 cm. Heads radiate, pedunculate, ca. 1.5 cm diam.; involucre campanulate, resinous, 8–10 × 8–18 mm; phyllaries in 4 to 6 unequal series, graduated, shortly acuminate, broadly elliptic to narrowly oblong, erect, 4–9 mm, subcoriaceous, with sessile glandular trichomes in pits; acumen flat, 2–3 mm, with sessile glandular trichomes. Ray florets 15 to 20; tube glabrous, ligule elliptic, 7–8 mm, apex entire or lobed. Disk florets with corolla 5–6 mm, with a gradually ampliate throat. Achenes yellowish or dull brownish, elliptic, 4-angled, 3–3.5 mm, striate, with a crown at the apex; pappus of 2 to 4 bristles, 3–5 mm, straight to somewhat curved, barbellate. Chromosome number: $n = 6$ (Pinkava & Keil, 1977: 681; Dunford, 1986: 302).

Iconography. Steyermark (1934: 505, fig. 20); Strother and Wetter (2006: 436).

Distribution and habitat. *Grindelia arizonica* has been found on rocky hillsides, tablelands, canyons, along streams, and prairies with pines and oaks, from 1600 to 2500 m, in Arizona, Colorado, and New Mexico (U.S.A.), and Chihuahua and Durango (Mexico).

Phenology. *Grindelia arizonica* flowers from July to August.

Etymology. The specific epithet refers to the state of Arizona in the United States, where the type specimen was collected.

Common name. Arizona gumweed (<http://plants.usda.gov/>).

Discussion. *Grindelia arizonica* is characterized by its radiate heads ca. 1.5 cm diameter, with erect phyllaries, and flat acumen, in unequal series. The glands of the leaves are sessile but are not located in pits.

Gray established the name *Grindelia arizonica*, with no description in 1882, for the specimen collected and described by J. T. Rothrock (1878:

141), who applied the name *G. microcephala*. Three varieties of *G. arizonica* established by Steyermark in 1934 (varieties *dentata*, *microphylla*, and *stenophylla*) have no taxonomic standing since the size and the margin of leaves—characters that distinguished the varieties for Steyermark—are variable within the species. Nesom (1990) included a fourth variety by Steyermark, *G. arizonica* var. *stenophylla*, as a synonym of *G. decumbens*, but this species has reflexed phyllaries and the glands of the leaves are in pits.

Additional specimens examined. MEXICO. **Chihuahua:** 29 km W of Colonia Alvaro, *J. L. Neff 8-19-91-3* (GH). **Durango:** dry fields S of town, *C. F. Baker, F. S. Earle & S. M. Tracy 538* (GH). U.S.A. **Arizona:** Coconino Co., 1/2 mi. N of mile marker 318 on state hwy. 209, *D. Walter & V. Walter 10549* (MO); Gila Co., mesa near Barnhart Creek, *R. E. Collom 463* (MO); Sierra Ancha, *G. J. Harrison & T. H. Kearney 8334* (US). **Colorado:** Archuleta Co., along US 84, *M. A. Wetter 1033* (NY); Pagosa Springs, *C. F. Baker 682* (GH); La Plata Co., 5.9 mi. E of La Plata–Montezuma Co. line, *M. A. Wetter 774* (NY); Montezuma Co., Mesa Verde Natl. Park, roadside, *J. A. Moore & J. A. Steyermark 3773* (MO); 2.35 mi. near Dolores, *M. A. Wetter 969* (NY). **New Mexico:** Río Arriba Co., Carson Natl. Forest, *M. A. Wetter 700* (NY); Sandoval Co., 10.6 mi. S of Sandoval–Río Arriba Co. line, *M. A. Wetter 955* (NY).

3. Grindelia camporum Greene, Man. Bot. San Francisco, 171. 1894. TYPE: U.S.A. California: Antioch, 5 Sep. 1881, *E. L. Greene s.n.* (lectotype, designated by Lane [1992: 216], MO-130218!).

Grindelia robusta Nutt. var. *rigida* A. Gray, Bot. California [W. H. Brewer] 1: 304. 1876. TYPE: U.S.A. California: Monte Diablo, 1860–1862, *W. H. Brewer 850* (lectotype, designated by Lane [1992: 216], GH [barcode] 00037709!).

Grindelia procera Greene, Man. Bot. San Francisco, 172. 1894. TYPE: U.S.A. California: San Joaquín Co., Banta, 9 Sep. 1892, *F. T. Bioletti s.n.* (lectotype, designated by Lane [1992: 216], UC [barcode] 32097 digital image!).

Grindelia bracteosa J. T. Howell, Madroño 2: 22. 1931, syn. nov. *Grindelia rubricaulis* DC. var. *bracteosa* (J. T. Howell) Steyerm., Ann. Missouri Bot. Gard. 21: 227. 1934. *Grindelia robusta* Nutt. var. *bracteosa* (J. T. Howell) D. D. Keck, Aliso 4: 102. 1958. *Grindelia camporum* Greene var. *bracteosa* (J. T. Howell) M. A. Lane, Novon 2: 216. 1992. TYPE: U.S.A. California: Orange Co., in hard clay soil, hills on N side of Santa Ana Canyon, 600 ft., 16 July 1927, *J. T. Howell 2786* (holotype, CAS [barcode] 00123700 digital image!; isotypes, CAS [barcode] 00123701 digital image!, RSA [barcode] 0001217 digital image!).

Grindelia camporum Greene var. *abbreviata* Steyerm., Ann. Missouri Bot. Gard. 21: 228. 1934. TYPE: U.S.A. California: Los Angeles Co., Lancaster, 23 Sep. 1927, *R. Hoffmann s.n.* (holotype, SBBG [barcode] 000062 digital image!).

Grindelia camporum Greene var. *australis* Steyerm., Ann. Missouri Bot. Gard. 21: 228. 1934. TYPE: U.S.A. California: Los Angeles Co., 3 mi. E of Elizabeth Lake, 4 Sep. 1928, *P. A. Munz & I. M. Johnston 11157* (holotype, RSA [barcode] 0001218 digital image!; isotype, MO-714105!).

Grindelia camporum Greene var. *parviflora* Steyerm., Ann. Missouri Bot. Gard. 21: 534. 1934. TYPE: U.S.A. California: Contra Costa Co., Liberty School on Marsh Creek Rd., 28 Sep. 1930, *J. T. Howell 5496* (holotype, CAS [barcode] 00123704 digital image!; isotypes, GH [barcode] 00037686!, MO-1015935!).

Grindelia rubricaulis DC. var. *elata* Steyerm., Ann. Missouri Bot. Gard. 21: 227. 1934, syn. nov. TYPE: U.S.A. California: Ventura Co., 7 mi. SW of Simi, 29 May 1931, *J. Jowell 6574* (holotype, CAS [barcode] 00123670 digital image!).

Perennial subshrubs to 1.5 m; stems 1 or several, erect, ramified, with sessile glandular trichomes. Leaves sessile, coriaceous, ovate to oblong, clasping; blade apex acute or obtuse, margin entire or toothed, teeth ending in a sclerotic tip, simple hairs absent or only at the margins, sessile glandular trichomes in pits on both blade surfaces; basal leaves 7–9 × 2–3 cm; cauline leaves progressively smaller. Heads radiate, pedunculate, 2–3 cm diam.; involucre hemispheric, resinous, 10–15 × 15–25 mm; phyllaries in 4 to 6 unequal series, graduated, acuminate; the outer and middle bracts narrowly ovate, spreading to reflexed, 4–6 mm, glabrous; acumen terete or subterete, curved, 2–3 mm, with sessile glandular trichomes in pits; the upper bracts narrowly elliptic, erect, shortly acuminate, 10 mm. Ray florets 15 to 40; tube glabrous, ligule elliptic to ovate, 8–15 mm, apex entire or toothed. Disk florets with corolla 6–7 mm, with a gradually ampliate throat. Achenes yellowish or dull brownish yellow, 2- or 3-angled, broadly elliptic, 3–5 mm, smooth, obliquely truncate or with a crown at the apex; pappus of 2 or 3 subulate scales, 3–7 mm, straight, smooth. Chromosome numbers: $n = 6$ (Dunford, 1986: 299, sub *Grindelia procera*; Lane & Li, 1993: 541); $2n = 12$ (Raven et al., 1960: 126; Semple et al., 1992: 53; Lane & Li, 1993: 541); $2n = 24$ (McLaughlin, 1986: 1748).

Iconography. Jepson (1925: 1021, fig. 924); Steyermark (1934: 540, fig. 29).

Distribution and habitat. *Grindelia camporum* has been collected from alluvial clay, sandy, or rocky soils, prairies, hillsides, roadsides, and disturbed sites, from 150 to 1400 m, in California (U.S.A.).

Phenology. *Grindelia camporum* flowers from March to October.

Etymology. The specific epithet is taken from the Greek "camphora-" or "camphor," which refers to the aromatic resin of the leaves.

Common name. Great Valley gumweed (<http://plants.usda.gov/>).

Discussion. Among the species from California, *Grindelia camporum* is quite distinctive by its coriaceous leaves with sessile glandular trichomes in pits on both blade surfaces, and by its heads with acuminate phyllaries, with terete or subterete and curved acumen, arranged in unequal series.

Three varieties, *Grindelia camporum* var. *abbreviata*, *G. camporum* var. *australis*, and *G. camporum* var. *parviflora*, were established by Steyermark (1934) and are here considered synonyms of *G. camporum*, since the size of leaves and heads and the number of ray florets—characters utilized by Steyermark for their differentiation—are variable within the species. Two other varieties of *G. camporum* described by Steyermark (1934), variety *davyi* (Jeps.) Steyerm. and variety *interioris* (Jeps.) Steyerm., are here referred to the synonymy of *G. humilis* Hook. & Arn. var. *humilis*, a species in which the phyllaries are subequal with the acumen triangular, flat or subterete, and as long as the base.

Strother and Wetter (2006) included *Grindelia camporum* in the synonymy of *G. hirsutula*. We do not agree with their taxonomic opinion because *G. hirsutula* has hirsute to lanuginous stems rather than the glandular trichomes seen in *G. camporum*. Further distinctions in *G. hirsutula* are the herbaceous or subcoriaceous leaves with simple hairs (vs. coriaceous with glandular trichomes), the sessile glandular trichomes that are not in pits (as in *G. camporum*), and the phyllaries that are subulate (vs. acuminate).

Another variety described by Steyermark (1934) under a different species, *Grindelia rubricaulis* var. *elata*, corresponds well to *G. camporum* with its resinous-punctate leaves and its acuminate phyllaries.

Grindelia bracteosa is newly referred to *G. camporum* herein, based on its leaves and involucre. In the type that has mature achenes, most of the ligulate flowers have fallen off, so its heads were described as having "all disk-flowers or rarely 1 or few minute ray-flowers." This is in agreement with Lane (1993), who referred to the name as the variety *G. camporum* var. *bracteosa*. She further noted that her variety was possibly derived from the hybrid *G. camporum* × *G. hirsutula* and *G. squarrosa* var. *serrulata* (Rydb.) Steyerm. (a name referred to *G. squarrosa* f. *squarrosa* in this paper).

Additional specimens examined. U.S.A. **California:** Alameda Co., Sunol, *D. Demaree 10522a* (MO); Mocho Creek, Livermore, *J. T. Howell 10827* (MO); along roadside, 1 mi. S of Mission San José, *E. A. Purer 5462* (MO); Colusa Co., Maxwell–Colusa Rd. just E of Two Mile Rd., ca. 2 mi. E of Maxwell, *V. Oswald 4410* (MO); Contra Costa Co., W of Tracy, *J. A. Moore & J. A. Steyermark 3683* (MO); Glenn Co., ditch betw. Norman & Willows on U.S. Hwy. 99, *A. A. Heller 15483* (MO); Sacramento Natl. Wildlife Refuge S of Willows, *V. Oswald 4408* (MO); Kern Co. betw. U.S. Hwy. 5 & canal on E side of hwy. just S of intersection of 1 & 5 ca. state hwy. 46, *M. A. Lane 3097* (MO); Los Angeles Co., El Segundo, *D. Demaree 10248* (MO); hills Los Angeles, July 1889, *H. E. Hasse s.n.* (MO-795951); ca. 0.25 mi. E of Green Valley Rd. on Elizabeth Lake Rd. (to Leona Valley & Palmdale), *M. A. Lane 3093* (MO); San Gabriel, *F. W. Peirson 8190* (MO); along roadside, *E. A. Purer 4994* (MO); Marin Co., San Anselmo, *J. T. Howell 11462* (MO); Ignacio, *J. T. Howell 11721* (MO); Mariposa Co., Mariposa, *J. T. Howell 8133* (MO); Merced Co., Merced, *J. T. Howell 5329* (MO); Monterey Co., Cypress Point, *L. S. Rose 33348A* (MO); Orange Co., Newport Beach, coast hwy., *C. B. Wolf 8101* (MO); San Diego Co., Oceanside, *S. B. Parish 4452* (MO); mi. N of Chula Vista, *E. A. Purer 5045* (MO); along hwy., Silver Strand Beach State Park, *E. A. Purer 5902* (MO); San Francisco Co., S San Francisco, *D. Demaree 10469* (MO); San Joaquin Co., 1 mi. W of San Joaquin River bridge near Lathrop, *J. T. Howell 5550* (MO); 9.5 mi. from Tracy on Tesla Rd., *J. T. Howell 10842* (MO); Corral Hollow Creek, 8 mi. from Tracy on Tesla Rd., *J. T. Howell 10849* (MO); Stockton, *E. E. Stanford 719* (MO); near Lathrop, *W. N. Suksdorf 8* (MO); San Luis Obispo Co., along CA State hwy. 58 to Santa Margarita, *M. A. Lane 3098* (PH); Santa Barbara Co., Summerland, *P. A. Munz 12916* (MO); Santa Clara Co., Alviso, *C. F. Baker 1701* (MO); Solano Co., Pleasant Valley, W of Vacaville, *A. A. Heller 16312* (MO); Montezuma Hills, *J. T. Howell 11648* (MO); Collinsville, *J. T. Howell 11692* (MO); Sonoma Co., 6 mi. from Sonoma, *s. coll.* (MO); Stanislaus Co., 1.5 mi. of Modesto, *J. T. Howell 4550* (MO); Ventura Co., coastal flat at Little Sycamore Creek, Malibu Hwy. to Oxnard, *J. T. Howell 6566* (MO).

4. Grindelia confusa Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 17(5): 442. 1938. TYPE: Mexico. Chihuahua: swale, Namiquipa plains, 17 Aug. 1936, *D. H. LeSueur 1016* (holotype, F [barcode] 0050294F digital image!; isotypes, MO-1265304!, PH [barcode] 00047853!, TEX [barcode] 00373588!). Figure 3.

Annual subshrubs, ca. 0.15 m; stems 1 to 8, erect, slender, ramified, with simple hairs and stipitate glandular trichomes. Leaves herbaceous, sessile, linear to narrowly ovate, pinnatisect; blade apex acute, margin toothed, the teeth ending in a sclerotic tip, with simple hairs and stipitate glandular trichomes on both blade surfaces; basal leaves 1.5–3.3 × 0.2–0.5 cm; cauline leaves progressively smaller. Heads radiate, pedunculate, 2.5–3 cm diam.; involucre hemispheric-campanulate, scarcely resinous, 7–8 × 13–15 mm; phyllaries in 4 or 5 unequal series, graduated, long acuminate, subcoriaceous, linear-elliptic, spreading to reflexed, 2–5 mm; acumen terete, 1–2.5 mm. Ray florets 25 to 31; tube glabrous, ligule elliptic, 8–12 mm, apex entire. Disk florets with corolla 4–5 mm, with a gradually ampliate throat. Achenes dull brownish yellow,

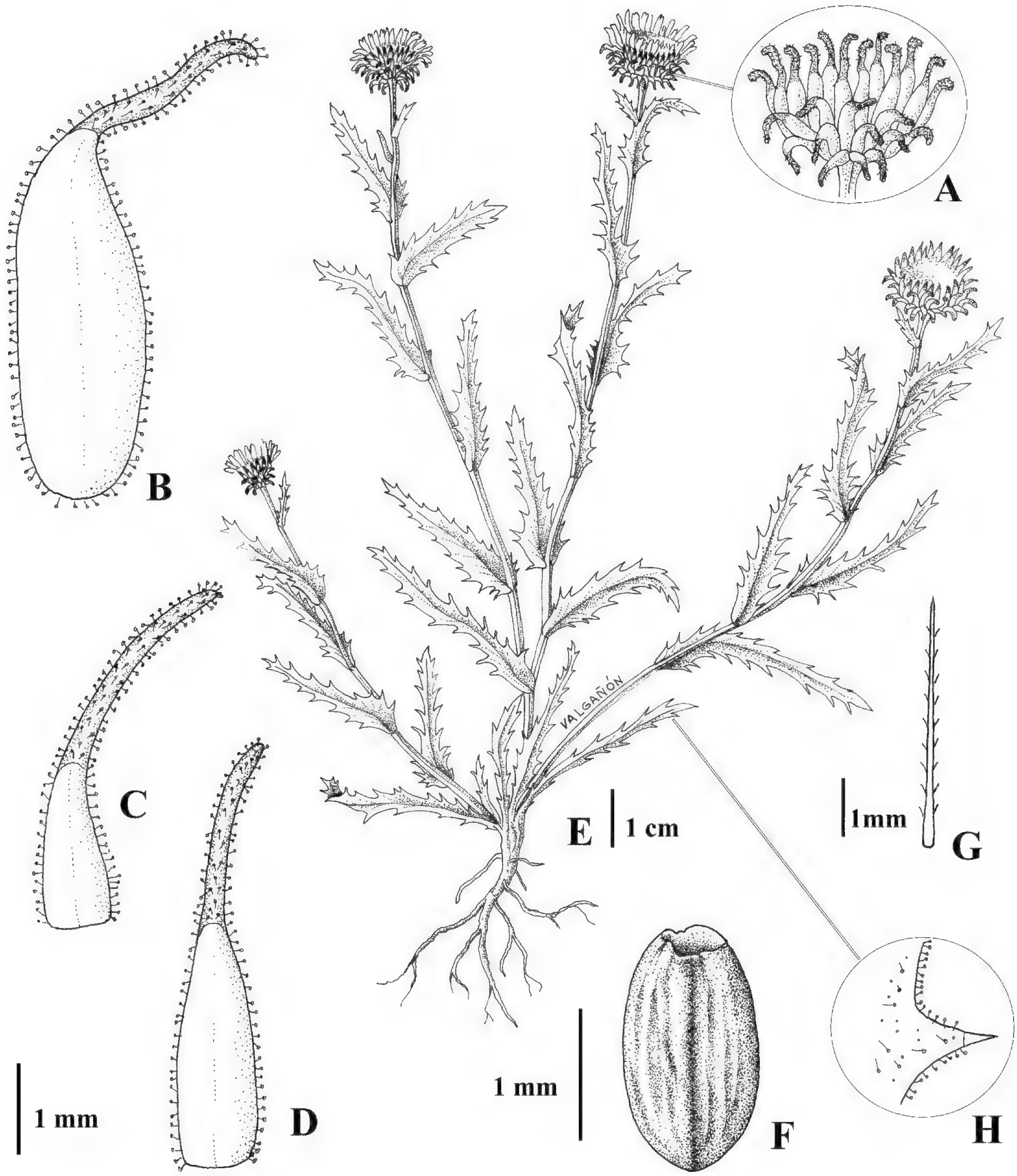

Figure 3. *Grindelia confusa* Steyerm. —A. Involucre, with phyllaries in four or five series. B–D. Representative phyllaries. —B. Inner series. —C. Outer series. —D. Middle series. —E. Fertile habit. —F. Achene, showing the longitudinal furrows. —G. Pappus, showing one of two barbellate bristles. —H. Leaf tooth, ending in a sclerotic tip, with simple hairs and stipitate glandular trichomes seen on both blade surfaces. Drawn from *M. A. Lane 2276 with R. Sanders* (TEX).

subquadrate to quadrate, 2–2.5 mm, smooth to deeply transverse or longitudinally furrowed, apex truncate; pappus of 2 bristles, straight, 3–4 mm, barbellulate. Chromosome number: $n = 6$ (Lane & Li, 1993: 541).

Distribution and habitat. *Grindelia confusa* has been collected from sandy and saline soils and humid grasslands, from 1800 to 2150 m, in Chihuahua, Durango, and Tamaulipas (Mexico).

Phenology. *Grindelia confusa* flowers from July to August.

Etymology. The specific epithet is taken from the Latin "confusum," meaning "uncertain." Steyermark

(1938) found this species different from the species monographed in 1934 and indicated his initial confusion.

Discussion. *Grindelia confusa* is an annual species that differs from the other Mexican species of *Grindelia* by its simple hairs and stipitate glandular trichomes, its herbaceous, pinnatisect leaves, and its phyllaries with a long and terete acumen, arranged in (four or five) unequal series.

Additional specimens examined. MEXICO. **Chihuahua:** Mpio. Valentín Gómez Farías, *T. Lebgue & E. Estrada 3316* (TEX). **Durango:** in slightly saline meadows, 19 mi. NE of Durango, rte. 31, *D. S. Correll & I. M. Johnston 20165* (TEX); 12.3 mi. W of town plaza of Guadalupe Victoria, on hwy. 40 & just W of Hernández, *M. A. Lane 2273 with R. Sanders* (TEX); 23.2 mi. W of Guadalupe Victoria (town plaza) & 11.3 rd. mi. W of San Francisco, I. Madero on hwy. 40, *M. A. Lane 2276 with R. Sanders* (TEX). **Tamaulipas:** Matamoros, 16 July 1980, *E. Guevara s.n.* (XAL).

5. Grindelia decumbens Greene, Pittonia 3: 102. 1896. TYPE: U.S.A. Colorado: Cimarron, 30 Aug. 1896, *E. L. Greene s.n.* (holotype, NDG-53581 digital image!; isotype, NDG-53582 digital image!).

Perennial subshrubs, 0.15–0.5 m, with conspicuous xylopodium; stems 3 to 8, prostrate with tips rising upward, ramified, glabrous. Leaves herbaceous, sessile, entire or pinnatisect, narrowly oblong to spatulate; blade apex acute, margin entire or toothed, teeth ending in a sclerotic tip, simple hairs absent, sessile glandular trichomes in pits on both blade surfaces; basal leaves 2–8 × 0.6–1.5 cm; cauline leaves clasping, progressively smaller. Heads radiate, pedunculate, 1.5–2 cm diam.; involucre hemispheric-campanulate, moderately resinous, 8–11 × 6–15 mm; phyllaries in 5 or 6 unequal series, graduated, acuminate, linear-elliptic to narrowly oblong, reflexed, 3–7 mm, glabrous; acumen triangular, subterete, erect, 1–1.5 mm, with sessile glandular trichomes in pits. Ray florets 12 to 24; tube glabrous, ligule narrowly elliptic, 7–12 mm, apex entire or toothed. Disk florets with corolla 5–6 mm, with a gradually ampliate throat. Achenes yellowish or dull brownish, elliptic, 3- or 4-angled, 3–3.5 mm, somewhat striate, apex truncate or knobby; pappus of 2 to 5 setiform awns, 3–5 mm, curved, barbellate to barbellulate. Chromosome number: $2n = 12$ (Whitaker & Steyermark, 1935: 71).

Iconography. Steyermark (1934: 540, fig. 18).

Distribution and habitat. *Grindelia decumbens* has been found on plains, slopes, and stream banks, from 200 to 3000 m, in Colorado and northern New Mexico (U.S.A.).

Phenology. *Grindelia decumbens* flowers from July to August.

Etymology. The specific epithet is taken from the Latin adjective "decumbens" or "prostrate," which refers to the habit of the species.

Common name. Reclined gumweed (<http://plants.usda.gov/>).

Discussion. *Grindelia decumbens* is characterized by its prostrate stem bases, leaves with sessile glandular trichomes in pits on both blade surfaces, and the hemispheric-campanulate involucre with reflexed, acuminate phyllaries.

Additional specimens examined. U.S.A. **Colorado:** T. 34 N, R. 3 W, *M. Ownbey 1403* (GH); Conejos Co., dry pasture land near Río Grande, turnoff to Los Pinos & Apache Canyon on State Hwy. 17, *R. G. Walter 4644* (MO); Ouray Co., 13 mi. N of Ouray, *J. A. Moore & J. A. Steyermark 3778* (MO); La Plata Co., Durango, *C. F. Baker, F. S. Earle & S. M. Tracy 497* (GH); Mineral Co., Santa María Reservoir, NW of Creede, *D. Walter & V. Walter 10742* (MO); Montrose Co., *J. A. Moore & J. A. Steyermark 3780* (MO). **New Mexico:** Río Arriba Co., Chama, *M. Hebard 2156A* (GH).

6. Grindelia fastigiata Greene, Pittonia 3: 102. 1896. TYPE: U.S.A. Colorado: Grand Jct., 27 Aug. 1896, *E. L. Greene s.n.* (holotype, NDG-53589 digital image!; isotype, NDG-53586-88 three digital images!).

Perennial subshrubs, 0.3–1.5 m; stems 2 to 4, erect, ramified, glabrous. Leaves sessile, subcoriaceous, oblong-spatulate to elliptic; blade apex acute or obtuse, margin entire, denticulate, or serrate, teeth ending in a sclerotic tip, glabrous, sometimes with margins scabrous, sessile glandular trichomes in pits on both blade surfaces; basal leaves 7–10 × 1.5–2 cm, blades attenuate into a pseudopetiole; cauline leaves clasping, 2.5–5 × 0.8–1.5 cm. Heads radiate or discoid, sessile or subsessile; involucre hemispheric-campanulate, resinous, 10–14 × 9–17 mm; phyllaries in 5 or 6 unequal series, graduated, acuminate, linear-elliptic to elliptic, reflexed, 3–9 mm, glabrous; acumen narrowly ovate, terete or subterete, strongly revolute, 1.5–2 mm, with sessile glandular trichomes. Ray florets present or absent. Disk florets with corolla 5–6 mm, with a gradually ampliate throat. Achenes dark brownish yellow, 2-angled, elliptic, 3.5–5 mm, smooth or striate, apex truncate or somewhat knobby; pappus of 2 or 3 setiform awns, 3–3.5 mm, straight, barbellulate.

Etymology. The specific epithet is taken from the Latin "fastigiatus," which refers to the branches being clustered, parallel, and erect.

Discussion. *Grindelia fastigiata* is characterized by its phyllaries arranged in (five or six) unequal series, with the acumen terete or subterete and strongly revolute. The taxon is morphologically similar to *G. nana*, with both taxa having leaves with sessile glandular trichomes in pits, with teeth ending in a sclerotic tip, and phyllaries with revolute acumen. *Grindelia fastigiata* differs from *G. nana* by its wider leaves (vs. leaves only to 1 cm wide), bigger heads (vs. only to 10 mm diameter), and 2-angled achenes (vs. 4-angled).

Strother and Wetter (2006) considered *Grindelia fastigiata* a synonym of *G. hirsutula*. Nevertheless, both species are quite different: the phyllaries are subulate in *G. hirsutula* (vs. acuminate in *G. fastigiata*), the achene apex forms a crown (vs. truncate in *G. fastigiata*), and the pappus is formed by somewhat curved, subulate scales (vs. setiform awns in *G. fastigiata*).

The following couplet distinguishes the two varieties of *Grindelia fastigiata*:

1a. Heads discoid ..... 6a. *G. fastigiata* var. *fastigiata*
1b. Heads radiate ..... 6b. *G. fastigiata* var. *revoluta*

6a. Grindelia fastigiata var. **fastigiata.**

Grindelia inornata Greene, Pittonia 3: 102. 1896, syn. nov. TYPE: U.S.A. Colorado: Cañon City, 7 Aug. 1896, *E. L. Greene s.n.* (holotype, NDG-53597 digital image!; isotypes, NDG-53587 digital image!, RM [barcode] 0001118 digital image!).

Grindelia inornata Greene var. *angusta* Steyerm., Ann. Missouri Bot. Gard. 21: 496. 1934, syn. nov. TYPE: U.S.A. Colorado: Colorado Springs, 1903, *H. L. Shantz 597* (holotype, US [barcode] 00127640 digital image!).

Heads discoid. Chromosome numbers: $n = 6$ (Dunford, 1986: 301, op. cit. sub *Grindelia inornata*); $2n = 12$ (Cronquist, 1994: 256).

Iconography. Cronquist (1994: 257).

Distribution and habitat. *Grindelia fastigiata* var. *fastigiata* has been found on prairies and along streams, ca. 1500 m, in Colorado (U.S.A.).

Phenology. *Grindelia fastigiata* var. *fastigiata* flowers from June to October.

Common name. Pointed gumweed (<http://plants.usda.gov/>).

Discussion. Steyermark (1934) differentiated *Grindelia fastigiata* from *G. inornata* by its longer and fastigiate branches. Nevertheless, there are intermediate specimens, e.g., *J. A. Moore & J. A. Steyermark 3770* and *3771* (both MO). Moreover, the leaves are widely variable within the species, and for this reason we also include the narrower-bladed *G. inornata* var. *angusta* within the synonymy of *G. fastigiata* var. *fastigiata*.

Additional specimens examined. U.S.A. **Colorado:** Denver Co., prairie, *I. W. Clokey 4324* (PH); Cheyenne Canyon, 21 Aug. 1915, *J. A. Drushel s.n.* (MO 782485); clay soil, *A. Eastwood 63* (MO); Denver, *J. H. Redfield 2964* (MO); El Paso Co., at W entrance for Manitou Springs, *M. A. Wetter 836* (NY); Fremont Co., Denver, 5 mi. E of Florence, *I. W. Clokey 4323* (MO); Cañon City, plants grown from *J. A. Moore & J. A. Steyermark 3183*, collected by Steyermark at MO (MO); Mesa Co., 6.4 mi. E of Colorado–Utah state line, *M. A. Wetter 568* (NY); Otero Co., 31 mi. NE of Las Animas–Otero Co. line, *M. A. Wetter 822* (NY). **Utah:** Emery Co., 5 mi. E of Woodside, desert near roadside, *J. A. Moore & J. A. Steyermark 3770* (MO); Grand Co., sand along Colorado River near Moab, *J. A. Moore & J. A. Steyermark 3771* (MO); N bank of Colorado River at hwy. 180 bridge, Moab, *M. P. Dunford 1173* (NY); ca. 1 mi. N of Professor Creek, Richardson Amphitheater, vic. Fisher Towers, along rd. to Fisher Valley, *S. L. Welsh 12631* (NY); Fisher Towers, *B. Franklin 4350* (NY).

6b. Grindelia fastigiata var. **revoluta** (Steyerm.) Adr. Bartoli & Tortosa, comb. et stat. nov. Basionym: *Grindelia revoluta* Steyerm., Ann. Missouri Bot. Gard. 21(3): 496–497, fig. 15. 1931. TYPE: U.S.A. Colorado: El Paso Co., along roadside, 14 mi. S from Colorado Springs, 1830 m, 30 Aug. 1931, *J. A. Moore & J. A. Steyermark 3784* (holotype, MO-1027335!).

Heads radiate, 2–3.5 cm diam. Ray florets 21 to 37; tube glabrous, ligule narrowly elliptic, 4–11 mm, apex entire or 2-toothed. Chromosome number: $n = 6$ (Dunford, 1986: 297, sub *Grindelia revoluta*).

Iconography. Steyermark (1934: 496, fig. 15).

Distribution and habitat. *Grindelia fastigiata* var. *revoluta* has been found on disturbed sites, roadsides, and sandy prairies, from 900 to 2300 m, in Colorado (U.S.A.).

Phenology. *Grindelia fastiagata* var. *revoluta* flowers from May to August.

Etymology. The name of *Grindelia fastigiata* var. *revoluta* is taken from the Latin "revolutus," meaning "rolled back," which refers to the phyllaries that roll from the apex toward the outside of the hemispheric-campanulate heads.

Discussion. We consider *Grindelia revoluta* simply a variety of *G. fastigiata* because the single difference between both species is the presence (or absence) of ray florets. Strother and Wetter (2006) also synonymized *G. revoluta*, but with *G. hirsutula* (see discussion under *G. fastigiata*).

Additional specimens examined. U.S.A. **Colorado:** El Paso Co., sandy prairie, 5 mi. E of Peyton, *J. A. Moore & J. A. Steyermark 3785* (MO); N of El Paso–Pueblo Co. line, *C. F. Craig & M. A. Wetter 1774* (NY); Palmer Lake, Rte. 85, *F. W. Pennell & R. L. Schaeffer Jr. 24683* (PH); at W entrance, archway for Manitou Springs, *M. A. Wetter 925* (NY); Mesa Co., plateau Creek Canyon, 1/2 mi. from I-70 at mouth of small side canyon on S side of creek, *D. Walter & V. Walter 11546* (MO); Pueblo Co., rest area betw. Pueblo & Colorado City, *M. A. Wetter 729* (NY); near St. Charles River, S side, *M. A. Wetter 920* (NY).

7. **Grindelia fraxinipratensis** Reveal & Beatley, Bull. Torrey Bot. Club 98: 334. 1971 [1972], as "fraxino-pratensis." [The hyphen use is a correctable orthographic error, fide Art. 60.9.]. TYPE: U.S.A. Nevada: Nye Co., 21 Aug. 1968, *J. L. Reveal 1887 with N. H. Holmgren* (holotype, US [barcode] 00008205!; isotypes, ARIZ-186626 digital image!, ASU [barcode] 0017179 digital image!, CAS [barcode] 00123705 digital image!, DS-644237 digital image!, G [barcode] 00223903 digital image!, LL [barcode] 00373589 digital image!, MICH [barcode] 1107421 digital image!, NY [barcode] 169602!, P [barcode] 00744054 digital image!, PH [barcode] 00047855 digital image!, RSA [barcode] 0001221 digital image!, SD [barcode] 00000096 digital image!, UC [barcode] 1395189 digital image!, WTU-286407 digital image!). Figure 4.

Perennial subshrubs, 0.5–1.2 m; stems 1 to 5, erect, slender, ramified, glabrous. Leaves subcoriaceous, sessile, narrowly elliptic; blade apex acute, margin entire or toothed, teeth ending in a sclerotic tip, simple hairs absent, sometimes margin scabrous, sessile glandular trichomes in pits on both blade surfaces; basal leaves 5–10 × 0.7–1.5 cm, blades attenuate into a pseudopetiole; blade apex acute or obtuse; cauline leaves clasping, 1.5–7 × 0.3–1.2 cm, apex acute. Heads radiate, pedunculate, 0.8–1.4 cm diam.; involucre obconic, resinous, 7–9 × 5–10 mm; phyllaries in 4 to 7 unequal series, graduated, acuminate, linear-elliptic to ovate, erect to spreading, 2–8 mm, glabrous; acumen triangular, erect, flat, 0.5–2 mm, with sessile glandular trichomes in pits. Ray florets 5 to 13; tube glabrous, ligule elliptic, 3–7 mm, apex entire or toothed. Disk florets with corolla 4–5.5 mm, with a gradually ampliate throat. Achenes yellowish, dull brownish, or dark brownish yellow, 4-angled, elliptic, 2.5–4 mm, striate, apex truncate to knobby; pappus of 2 bristles, 3–4 mm, smooth. Chromosome number: $2n = 24$ (Lane, 1993: 272).

Distribution and habitat. *Grindelia fraxinipratensis* grows on prairies and edges of forests, from 600 to 800 m, in California and Nevada (U.S.A.).

Phenology. *Grindelia fraxinipratensis* flowers from June to October.

Etymology. The specific epithet is taken from the Latin "fraxinipratensis," meaning "growing in the fields of ash trees."

Common name. Ash meadows gumplant (<http://plants.usda.gov/>).

Discussion. *Grindelia fraxinipratensis* is quite distinct from other North American species of *Grindelia* by its small radiate heads remarkable for their obconic involucre. Heads in other *Grindelia* are more often hemispheric to urceolate or campanulate in their overall appearance.

Additional specimens examined. U.S.A. **California:** Inyo Co., Amargosa, 20 Oct. 1968, *J. Beatley s.n.* (MO-2425710); Ash Meadows, *J. L. Reveal 1536* (MO); alkaline flat, W Ash Meadows Rd., NW of Ash Meadows Lodge, *J. L. Reveal 2107* (GH, MO); open meadows & woodland border, 8 Oct. 1970, *J. Beatley s.n.* (GH).

8. **Grindelia grandiflora** Hook., Bot. Mag. 78(ser. 3, vol. 8): pl. 4628. 1852. *Grindelia squarrosa* (Pursh) Dunal var. *grandiflora* (Hook.) A. Gray, Smithsonian Contr. Knowl. 3: 98. 1852. TYPE: [U.S.A.] Cult. in Hort. Kew from seeds collected in Texas, s.d., *Wright s.n.* (holotype, K-000250073 digital image!).

Grindelia costata A. Gray, Proc. Amer. Acad. Arts 17: 208, 1882. TYPE: Mexico. Coahuila: 23–24 Sep. 1880 [label, Feb–Oct. 1880], *E. Palmer 472* (holotype, GH [barcode] 00008445!; isotypes, K [barcode] 000221373 digital image!, NY [barcode] 00169631!, US [barcode] 00127636 digital image!).

Annual subshrubs, 0.5–1.5 m; stem 1, erect, ramified, glabrous. Leaves herbaceous, sessile, ovate, 2.5–6 × 0.5–0.15 cm, base cordate, clasping; blade apex acute to acuminate, margin with rounded teeth ending in a group of sessile glandular trichomes, occasionally entire in cauline leaves, simple hairs absent, sessile glandular trichomes on both blade surfaces. Heads radiate, pedunculate, 2.5–3 cm diam.; involucre hemispheric, scarcely resinous, 6–8 × 10–15 mm; phyllaries in 5 or 6 unequal series, graduated, acuminate, 3-nerved, with sessile glandular trichomes; the outer bracts linear-elliptic, 4 mm, erect to spreading, acumen filiform, subterete, erect, 2–3 mm; the middle and upper bracts elliptic, 5–7 mm, erect; acumen terete, erect, 1 mm. Ray florets 17 to 26; tube glabrous, ligule elliptic, 10–12 mm, apex entire or scarcely toothed. Disk florets with corolla 6–7 mm, with an abruptly ampliate throat. Achenes dull brownish or brownish yellow, monomorphic, broadly elliptic, 2- or 3-angled, 3–4 mm, longitudinally

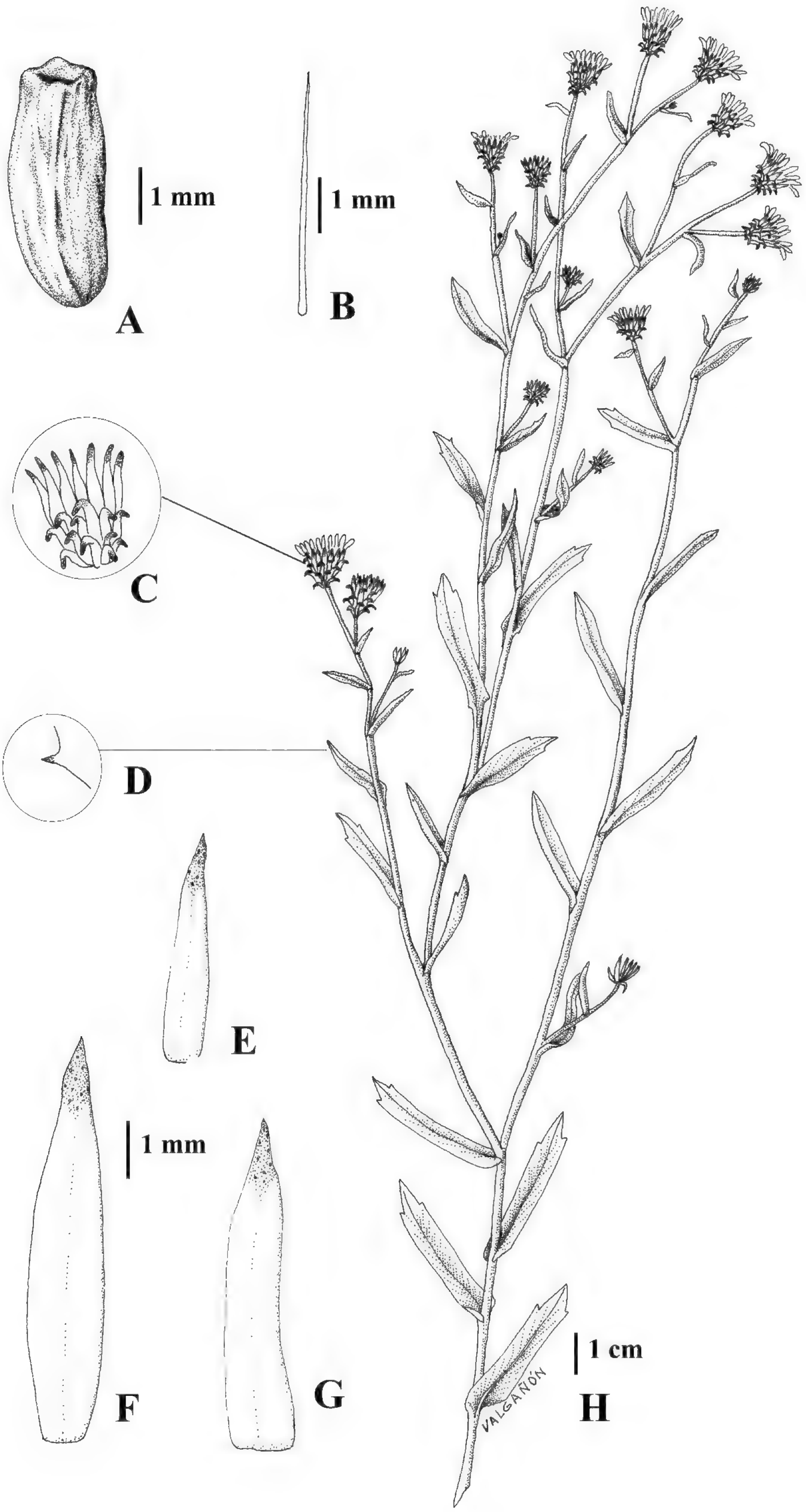

Figure 4. *Grindelia fraxinipratensis* Reveal & Beatley. —A. Achene, 4-angled, striate. —B. Pappus, showing one of two smooth bristles. —C. Involucre, with phyllaries in four to seven series. —D. Leaf tooth, ending in a sclerotic tip. B–D to same 1 mm scale. E–G. Representative phyllaries. —E. Outer series. —F. Inner series. —G. Middle series. —H. Fertile habit. Drawn from *J. L. Reveal 1536* (MO).

striate or furrowed, apex knobby or forming a crown; pappus of 2 bristles, 3–4.5 mm, straight, smooth to barbellulate. Chromosome numbers: $n = 6$ (Pinkava & Keil, 1977: 681; Dunford, 1986: 301); $2n = 12$ (Dunford, 1969: 20; Pinkava & Keil, 1977: 681; Zhao & Turner, 1993: 650).

Iconography. Steyermark (1934: 462, fig. 5).

Distribution and habitat. *Grindelia grandiflora* has been collected from disturbed and sandy soils, in roadsides, open forests, prairies, and streams, from 300 to 1200 m, in Texas (U.S.A) and Coahuila (Mexico).

Phenology. *Grindelia grandiflora* has been collected in flower from the beginning of July to October.

Etymology. The specific epithet refers to the size of the heads, from the Latin "grandiflorus," meaning "big flowers."

Common name. Many-ray gumweed (<http://plants.usda.gov/>).

Discussion. *Grindelia grandiflora* is characterized by its annual habit and phyllaries with a filiform acumen. Asa Gray considered this species only a variety of *G. squarrosa*. Both species differ in the sessile glandular trichomes (located in pits in the leaves of *G. squarrosa* vs. not in pits in *G. grandiflora*). The acumen of phyllaries ranges from linear to narrowly triangular, terete to subterete in *G. squarrosa* (vs. the noteworthy filiform, subterete acumen in *G. grandiflora*). The pappus consists of curved, setiform awns in *G. squarrosa* (vs. smooth to barbellate bristles in *G. grandiflora*), and the corolla of disk flowers has a gradually ampliate throat in *G. squarrosa* (vs. abruptly ampliate in *G. grandiflora*).

Additional specimens examined. MEXICO. **Coahuila:** Arteaga, Exposición E de la Sierra La Viga, El Zorrillo, *J. A. Encina 821 with J. A. Portillo* (ASU [barcode] 0018162); Sierra de las Alasanas al noroeste del ejido Mesa de las Tablas, *J. A. Encina 826 with S. Cruz J. & E. López* (ASU [barcode] 0018163); Muzquiz, roadside swamp, *T. Reeves & D. J. Pinkava P13009* (ASU [barcode] 0018164). U.S.A. **Texas:** Crockett Co., N part of Ozona, *V. L. Cory 40706* (GH); Edwards Co., Ranch Exp. Station, *V. L. Cory 5013* (MO); Fremont, laned county rd., line Sutton Co., 24 air mi. SSE of Sonora, *V. L. Cory 52450* (PH); Río Grande Co., Río Grande valley below Doñana, 1879, *C. C. Parry et al. s.n.* (GH); Sutton Co., SE part of Sonora, *V. L. Cory 50544* (US); arroyo in S part of town at end of Poplar St., *M. P. Dunford & C. C. Freeman 1157* (MO); E of Sonora, *M. A. Wetter 1012* (NY); Tarrant Co., rocky hillsides, *A. Ruth 64* (NY); Val Verde Co., along Devils River, 13 Sep. 1900, *H. Eggert s.n.* (MO-129986).

9. Grindelia greenmanii Steyerm., Ann. Missouri Bot. Gard. 21: 460. 1934. TYPE: Mexico. Coahuila: Lerios, mtn. section 15 leagues E of Saltillo, 10,000 ft., 10–13 July 1880, *E. Palmer 471* (holotype, GH [barcode] 00008448!; isotypes, K [barcode] 000221374 digital image!, NY [barcode] 00169633 digital image!, PH [barcode] 00047857 digital image!, US [barcode] 00931357 digital image!).

Grindelia vetimontis G. L. Nesom, Phytologia 68: 330. 1990, syn. nov. TYPE: Mexico. Nuevo León: Mpio. Zaragoza, Cerro El Viejo, 15 mi. W Dulces Nombres, 18 Aug. 1948, *F. G. Meyer & D. J. Rogers 2988* (holotype, MO-193880!; isotype, F [barcode] 1587883F digital image!).

Rhizomatous perennial subligneous subshrubs, 0.25–0.5 m; stems several, erect, ramified or not, with simple long hairs and generally also with stipitate glandular trichomes. Leaves herbaceous, sessile, oblong-elliptic, 2–11 × 0.5–1.2 cm; blade apex obtuse to acuminate, margin denticulate to finely serrate, teeth ending in a sclerotic tip, simple hairs and stipitate glandular trichomes on both blade surfaces; basal leaves with blades attenuate into a pseudopetiole; cauline leaves clasping, progressively smaller. Heads radiate, sessile, 2–4 cm diam.; involucre hemispheric-campanulate, scarcely resinous, 12–14 × 22–25 mm; phyllaries in 4 or 5 subequal series, acuminate, herbaceous, linear to linear-elliptic, erect to spreading, 8–11 mm, glabrous, margin entire; acumen triangular, flat to subterete, shorter than the base, 3–4 mm, with stipitate glandular trichomes. Ray florets 25 to 30; tube with stipitate glandular trichomes, ligule elliptic, 12–16 mm, apex entire. Disk florets with corolla 5–7 mm, with an abruptly ampliate throat. Achenes brownish, elliptic, 2-angled, flattened, 2.5–3 mm, smooth or slightly rugose, apex truncate; pappus of 2 or 3 bristles, 5–7 mm, smooth. Chromosome number: $n = 6$ (Pinkava & Keil, 1977: 681).

Iconography. Steyermark (1934: 460, fig. 4).

Distribution and habitat. *Grindelia greenmanii* grows in open forests of *Pinus* L. and *Picea* Link., from 2200 to 3650 m, in Coahuila, Nuevo León, and Tamaulipas (Mexico).

Phenology. *Grindelia greenmanii* flowers from June to December.

Etymology. *Grindelia greenmanii* was named in honor of Jesse More Greenman (1867–1951), curator of the Missouri Botanical Garden, who studied tropical flora, particularly from Mexico.

Discussion. *Grindelia greenmanii* is different from other *Grindelia* species with a rhizomatous habit, such as *G. obovatifolia* and *G. robinsonii*, with its larger

heads to 4 cm diameter (vs. no more than 2.5 cm diameter in the other two species), and by its phyllaries in subequal series (vs. unequal, graduated series).

When Nesom described *Grindelia vetimontis* in 1990, he stated that this species was allied to *G. greenmanii*, but differed by its eglandular stems and smaller leaves and heads. Nonetheless, we observed intermediate specimens, collected in Cerro Peña Nevada (*G. L. Nesom 4800*, TEX; *D. E. Breedlove 63552*, TEX), and the species name is synonymized.

Additional specimens examined. MEXICO. **Coahuila:** Sierra Coahuilon, *S. Ginzbarg et al. 180* (TEX); Cerro La Viga, *G. B. Hinton 20205* (MEXU); El Paso, *G. B. Hinton et al. 24382* (TEX); Arteaga, Sierra Coahuilon, *G. B. Hinton 20996* (MEXU); Arteaga, Sierra Los Camargos, *G. B. Hinton et al. 18344* (XAL); Los Lirios a El Cercado, 2405 m, *G. B. Hinton et al. 25428* (MEXU, TEX). **Nuevo León:** Mpio. Monterrey, 18 de Marzo, Cerro Potosí, below the summit on cobble roadside, 3429 m, *E. M. Chittenden 104* (TEX); Cerro El Potosí, 2750 m, *F. Garza & E. Estrada 4265* (TEX); Mpio. de Galeana, Las Canoas on Cerro Potosí, *C. H. Mueller 2173* (MO); ca. 37 km ENE of Dr. Arroyo, S-trending trail to summit of Cerro Peña Nevada beginning near rd. jct., *G. L. Nesom 4800* (TEX); 2.7 mi. S of San Francisco Javier on rd. betw. San Rafael Jct. & Galeana, on NE side of Cerro Potosí, *G. L. Nesom & J. Norris 7198* (TEX); El Lorito, *G. B. Hinton et al. 19831* (MEXU), *G. B. Hinton 19865* (MEXU); summit Cerro El Potosí, *G. B. Hinton et al. 25335* (MEXU); 18 Marzo to El Lorito, *G. B. Hinton 25388* (MEXU); Mpio. Zaragoza, Cerro El Viejo, *G. B. Hinton et al. 22434* (MEXU). **Tamaulipas:** along logging rd. E of Miquihuana on ridge SE of Cerro Peña Nevada, *D. E. Breedlove 63552* (TEX).

10. Grindelia hallii Steyerm., Ann. Missouri Bot. Gard. 21: 229. 1934, as "Hallii." *Grindelia hirsutula* Hook. & Arn. var. *hallii* (Steyerm.) M. A. Lane, Novon 2: 216. 1992. TYPE: U.S.A. California: San Diego Co., open ridges about Cuyamaca Lake, 30 June 1903, *L. Abrams 3957* (holotype, NY [barcode] 169603!; isotypes, CAS [barcode] 00123706 digital image!, DS-7262 digital image!, F [barcode] 0050285F digital image!, GH [barcode] 00008425!, MO [barcode] 714101 digital image!, RSA [barcode] 0001223 digital image!).

Perennial subligneous subshrubs, 0.25–0.6 m, with xylopodium; stems several, erect, slender, ramified, glabrous. Leaves subcoriaceous, sessile, narrowly elliptic, apex acute, margin entire or toothed, teeth ending in a sclerotic tip, simple hairs absent, sometimes margin scabrous, sessile glandular trichomes in pits on both blade surfaces; basal leaves narrowly obovate, 7–9 × 0.8–1 cm, blades attenuate into a pseudopetiole; blade apex acute or obtuse; cauline leaves elliptic to narrowly elliptic, 2–3.5 × 0.5–1 cm, clasping, apex acute. Heads radiate, pedunculate, 1.5–2 cm diam.; involucre hemispheric to hemispheric-campanulate, resinous, 8–15 × 12–15 mm; phyllaries in 5 unequal series, graduated, subulate, with sessile glandular trichomes; the outer bracts linear-elliptic, spreading to reflexed, 2 mm, apex flat, 1 mm; the middle bracts ovate-triangular, spreading, 4–6 mm, apex terete or subterete, 2–2.5 mm; the upper bracts elliptic, erect, 6–8 mm. Ray florets 10 to 20; tube glabrous, ligule elliptic, 8–9 mm, apex entire or toothed. Disk florets with corolla 6–7 mm, with a gradually ampliate throat. Achenes light brown, elliptic, 2- or 3-angled, 4–5 mm, smooth to furrowed, apex with a tooth or obliquely truncate; pappus of 2 bristles, 2.5–4 mm, smooth to barbellulate. Chromosome number: $n = 6$ (Raven et al., 1960: 126; Lane & Li, 1993: 541, sub *G. hirsutula* var. *hallii*).

Iconography. Steyermark (1934: 520, fig. 25).

Distribution and habitat. *Grindelia hallii* has been collected from rocky hillsides, from 1400 to 1700 m, in southern California (U.S.A.).

Phenology. *Grindelia hallii* flowers from July to October.

Etymology. *Grindelia hallii* was named in honor of Harvey Monroe Hall (1874–1932), a pioneer in experimental taxonomy and an authority on the study of Asteraceae in southern California.

Common name. San Diego gumplant (<http://www.calflora.org>).

Discussion. With its radiate heads with the involucre composed of subulate phyllaries in a graduated series, *Grindelia hallii* is related to *G. oxylepis*. The two taxa differ by the achenes being elliptic and smooth to furrowed, with the apex toothed or obliquely truncate in *G. hallii*. The achenes are subquadrate and tuberculate, with the apex truncate or forming a crown in *G. oxylepis*.

Grindelia hallii was reduced in rank as a variety of *G. hirsutula* by Lane (1992) and was later synonymized to this species by Strother and Wetter (2006). However, *G. hallii* has smaller heads, to 2 cm in diameter, in contrast to the significantly larger heads of *G. hirsutula* that range from 3.5–4 cm in diameter. *Grindelia hallii* has leaves with sessile glandular trichomes located in pits and simple hairs are absent; in *G. hirsutula*, the sessile glandular trichomes are not in pits and simple hairs are present.

Additional specimens examined. U.S.A. **California:** San Diego Co., Julian, *H. P. Chandler 5460* (NY); Cuyamaca Lake, Cuyamaca, *P. A. Muñiz & E. K. Balls 17997* (NY); along CA State hwy. 79, 2.7 mi. SE of California State hwy. 78 in Julian, *M. A. Lane 3088* (MO); Julian, Oct. 1889, *C. R. Orcutt s.n.* (MO-130078); Larkens, 80 mi. E, southern

part of San Diego Co., *E. Palmer 128* (MO); Cuyamaca Lake, *F. W. Peirson 4825* (MO); near Julian, 11 Aug. 1886, *C. R. Orcutt s.n.* (MO-130079); 40 mi. E of San Diego, Corte Madera Ranch, Pine Valley, *H. Van der Werff 6058* (MO); Pine Valley, ca. 50 mi. E of San Diego on Corte Madera Ranch, *H. van der Werff 8707* (MO).

11. Grindelia havardii Steyerm., Ann. Missouri Bot. Gard. 21: 474. 1934. TYPE: U.S.A. Texas: Culberson Co., Guadalupe Mtns., dry gravelly wash near mouth of McKittrick Canyon, 2000 m, 23 July 1931, *J. A. Moore 3607 with J. A. Steyermark* (holotype, MO [barcode] 714098!; isotypes, GH [barcode] 00008425!, MO [barcode] 714097 digital image!, MO [barcode] 714099 digital image!, MO [barcode] 714100 digital image!, NY [barcode] 169604!, P [barcode] 00742797 digital image!, RM [barcode] 0001121 digital image!, TEX [barcode] 147304 digital image!).

Perennial subshrubs, 0.3–1.5 m; stems 1 to several, erect, ramified, glabrous or hispid. Leaves subcoriaceous, sessile; blade apex obtuse or acute, margin crenate or toothed, teeth ending in a group of sessile glandular trichomes, simple hairs and sessile glandular trichomes present on both blade surfaces, and stipitate glandular trichomes only along the middle nerve; basal leaves obovate to oblong, 5.5–6 × 1.3–1.5 cm, blades attenuate into a pseudopetiole; leaves apex obtuse; cauline leaves ovate, 2.5–3 × 1–1.5 cm, clasping, auriculate; blade apex acute. Heads radiate, pedunculate, 2.5 cm diam.; involucre hemispheric, resinous, 8–13 × 12–22 mm; phyllaries in 5 or 6 unequal series, graduated, acuminate, with sessile glandular trichomes; the outer and middle bracts linear-elliptic, 4–10 mm, spreading to reflexed; acumen subterete to terete, 2–3.5 mm; the upper phyllaries narrowly elliptic, erect, shortly acuminate. Ray florets 18 to 25; tube glabrous, ligule narrowly oblong, 9–11 mm, apex entire. Disk florets with corolla 6–7 mm, with a gradually ampliate throat. Achenes light brown, elliptic, 2- or 3-angled, 4–5 mm, smooth to furrowed, apex with a tooth or obliquely truncate; pappus of 2 bristles, 4–7 mm, smooth to barbellulate. Chromosome numbers: $n = 6$ (Dunford, 1986: 297); $2n = 12$ (Powell & Powell, 1978: 161).

Iconography. Steyermark (1934: 476, fig. 11).

Distribution and habitat. Grindelia havardii grows on degraded, alluvial soils, and rocky hills, from 1300 to 2000 m, in Texas and New Mexico (U.S.A.), and Coahuila (Mexico).

Phenology. Grindelia havardii has been collected in flower from the beginning of June to December.

Etymology. Grindelia havardii was named in honor of the American botanist, Valery Havard (1846–1927). She published numerous articles on the flora of the states of Montana, the Dakotas, Texas, and Colorado.

Common name. Havard's gumweed (<http://www.nature.british-towns.net/>).

Discussion. Grindelia havardii is characterized by its large radiate heads with the acuminate phyllaries arranged in unequal series, with flat acumen, and leaves with teeth ending in sessile glandular trichomes.

M. A. Wetter annotated in type sheets (GH and MO) the transfer of *Grindelia lanceolata* var. *havardii* (Steyerm.) Wetter, but *G. lanceolata* differs from *G. havardii* in their smaller heads with phyllaries arranged in subequal series, linear, terete acumen, and leaves with teeth ending in a curved spinule.

Additional specimens examined. MEXICO. **Coahuila:** roadside ca. 3 mi. SE of Ocampo, *I. M. Johnston 8881* (GH). U.S.A. **New Mexico:** Chaves Co., 35 mi. W of Roswell, *F. S. Earle & E. S. Earle 509* (MO). **Texas:** Culberson Co., Pratt Ranch, *B. E. McKechnie 283* (MO); Jeff Davis Co., Davis Mtns., dry rocky hillside above Little Ajuga Canyon, *J. A. Moore & J. A. Steyermark 3151* (MO).

12. Grindelia hintoniorum G. L. Nesom, Phytologia 68: 328. 1990. TYPE: Mexico. Nuevo León: Mpio. Galeana, E of Pablillo, oak woods, 1940 m, 15 May 1984, *G. B. Hinton et al. 18666* (holotype, TEX [barcode] 00373591!; isotypes, ASU [barcode] 0017180 digital image!, MEXU-GBH 18666 digital image!, US [barcode] 00406463 digital image!). Figure 5.

Perennial subshrubs, 0.05–0.15 m, with xylopodium; stems several, prostrate with tips rising upward, not ramified, with scattered simple hairs and dense stipitate glandular trichomes. Leaves herbaceous, sessile; blade apex acute or obtuse; margin entire or crenate, teeth ending in a sclerotic tip, blade with simple hairs along the nerves, dense stipitate glandular trichomes on both blade surfaces; basal leaves spatulate-obovate, 5–7 × 0.5–0.6 cm, attenuate into a pseudopetiole; blade apex acute; cauline leaves oblong-elliptic, 1–2.2 × 0.35–0.4 cm, clasping, blade apex obtuse. Heads radiate, pedunculate, 1–1.2 cm diam.; involucre hemispheric, resinous, 7–8 × 7–9 mm; phyllaries in 5 or 6 subequal series, subulate, triangular to narrowly triangular, glabrous, apex flat to subterete, minutely aristate, with stipitate glandular trichomes; the outer bracts spreading to scarcely reflexed, 4–4.5 mm; the middle bracts spreading to erect, 5–6 mm; the upper

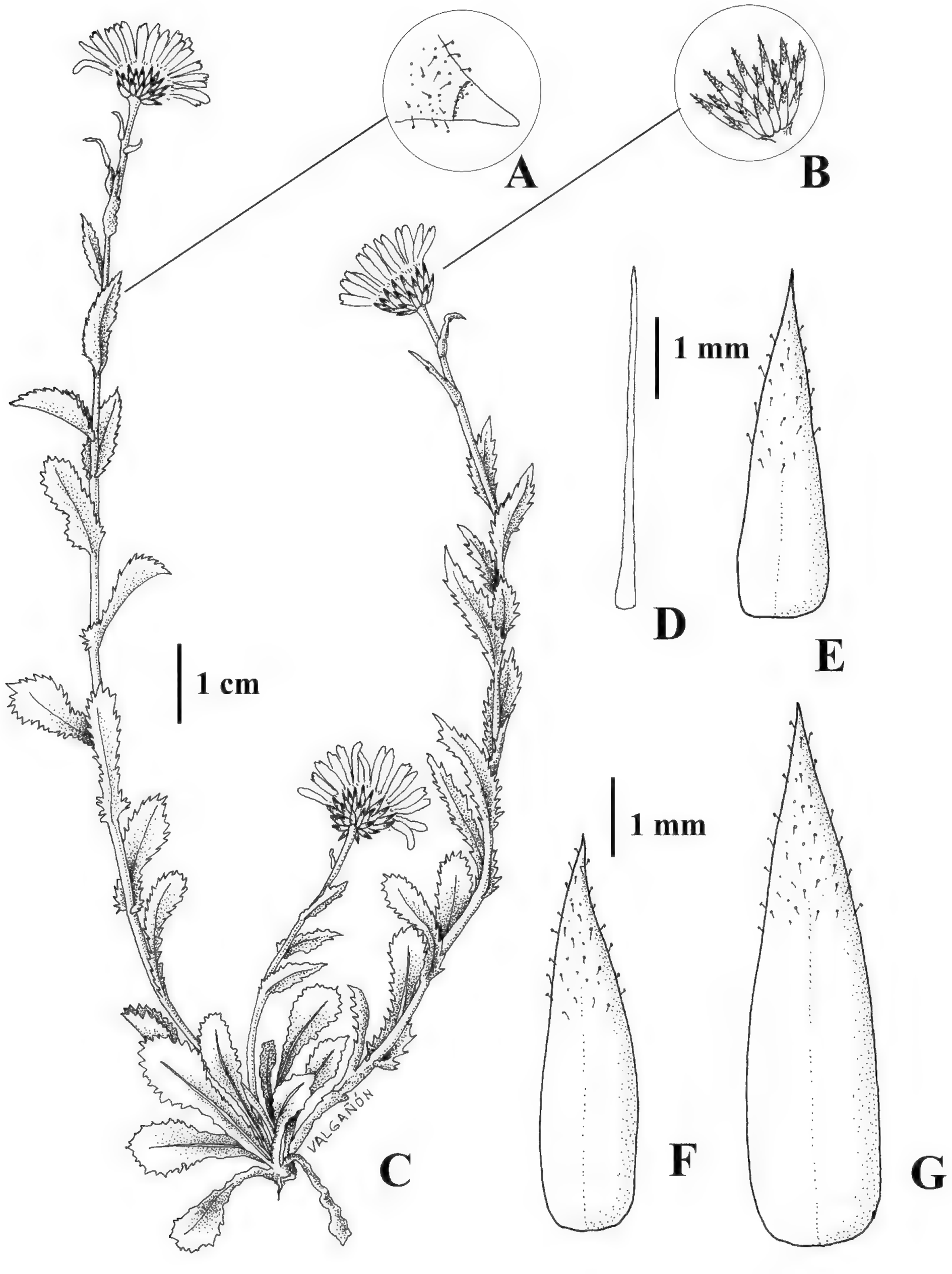

Figure 5. *Grindelia hintoniorum* G. L. Nesom. —A. Leaf tooth, ending in a sclerotic tip, the blade surfaces with dense stipitate glandular trichomes. —B. Part of the involucre; outer phyllary series represented. —C. Fertile habit. —D. Pappus, showing one of two smooth bristles. E–G. Representative phyllaries. —E. Outer series. —F. Middle series. —G. Inner series. D–G to same 1 mm scale. Drawn from *M. Taylor 24* (HB).

phyllaries erect, 7–8 mm. Ray florets 19 to 34; tube glabrous, ligule narrowly elliptic, 9–11 mm, apex entire. Disk florets with corolla 4.5–5 mm, with an abruptly ampliate throat. Achenes not seen; pappus of 2 bristles, smooth. Chromosome number not known.

Distribution and habitat. *Grindelia hintoniorum* has been collected in calcareous soils, in *Quercus* L. forests and cultivated lands, in Nuevo León (Mexico).

Phenology. *Grindelia hintoniorum* flowers from June to September.

Etymology. *Grindelia hintoniorum* was named in honor of George B. Hinton (1882–1943), collector of plants in southwestern Mexico.

Discussion. *Grindelia hintoniorum* is quite a distinctive species, represented by dwarf plants not exceeding 15 cm and with a xylopodium. The stems and leaves are densely covered by stipitate glandular trichomes; the radiate heads are small, with phyllaries arranged in unequal series, and the acumen flat.

Additional specimens examined. MEXICO. **Nuevo León:** Mpio. Galeana, encinal, Pablillo, Sierra Madre Oriental, *F. W. Pennell 17006* (PH); hacienda, Pablillo, *M. Taylor 24* (PH); 9 km S of San Rafael along hwy. 57 toward San Roberto Jct., Broad Valley (Valle de Potosí), *G. L. Nesom, M. Mayfield & G. B. Hinton 7587* (MO).

13. Grindelia hirsutula Hook. & Arn., Bot. Beechey Voy. 147. 1833. TYPE: U.S.A. California: [probably from San Francisco Bay to Monterey Bay, cf. A. Gray, Geol. Surv. Calif. Bot. 1: 304. 1876.] s.d., *Botany Beechey's Voyage s.n.* (holotype, E [barcode] 00369114 digital image!; isotypes, K [barcode] 000250075 digital image!, UC [barcode] 292620 digital image!).

Grindelia rubricaulis DC., Prodr. (DC.) 5: 316. 1836. *Grindelia hirsutula* Hook. & Arn. subsp. *rubricaulis* (DC.) D. D. Keck, Aliso 4: 102. 1958. TYPE: U.S.A. California: 1833, *D. Douglas 55* (holotype, G-DC, IDC microfiche!; isotypes, BM [barcode] 001025308 digital image!, GH [barcode] 00037710 digital image!, K [barcode] 000250076 digital image!, UC [barcode] 292723 digital image!).

Grindelia pacifica M. E. Jones, Bull. Torrey Bot. Club 9: 31. 1882, as "Pacifica." TYPE: U.S.A. California: Santa Cruz Co., on hills at Santa Cruz, 1881, *M. E. Jones s.n.* (holotype, RSA [barcode] 0001227 digital image!; isotypes, GH [barcode] 00037707!, NY [barcode] 8411!).

Grindelia patens Greene, Pittonia 2: 290. 1892. *Grindelia robusta* Nutt. var. *patens* (Greene) Jeps., Fl. W. Calif. 554. 1901. *Grindelia hirsutula* Hook. & Arn. f. *patens* (Greene) Steyerm., Ann. Missouri Bot. Gard. 21: 570. 1934. TYPE: U.S.A. California: Berkeley, July 1881, *E. L. Greene s.n.* (holotype, NDG-53625 digital image!; isotype, F [barcode] 0050291F digital image!).

Grindelia hirsutula Hook. & Arn. f. *cacumena* Steyerm., Ann. Missouri Bot. Gard. 21: 572. 1934, syn. nov. TYPE: U.S.A. California: Oakland Hills, 2000 ft., 1866, *H. N. Bolander 389* (holotype, US [barcode] 00008206 digital image!; isotypes, NY [barcode] 00169609!, NY [barcode] 00169610!).

Grindelia hirsutula Hook. & Arn. var. *brevisquama* Steyerm., Ann. Missouri Bot. Gard. 21: 572. 1934. TYPE: U.S.A. California: Sonoma Co., Black Point Rd., 13 July 1930, *J. T. Howell 5338* (holotype, CAS [barcode] 00123707 digital image!; isotype, UC [barcode] 473549 digital image!).

Grindelia hirsutula Hook. & Arn. f. *glabrata* Steyerm., Ann. Missouri Bot. Gard. 21: 573. 1934, syn. nov. [described under *Grindelia hirsutula* var. *brevisquama*]. TYPE: U.S.A. California: Sonoma Co., 8 mi. W of Petaluma, 8 June 1930, *J. T. Howell 5221* (holotype, MO-1016008!; isotypes, CAS [barcode] 00123708 digital image!, GH [barcode] 00037693!, RSA [barcode] 0001224 digital image!).

Grindelia hirsutula Hook. & Arn. f. *pedunculoides* Steyerm., Ann. Missouri Bot. Gard. 21: 574. 1934, syn. nov. [described under *Grindelia hirsutula* var. *brevisquama*]. TYPE: U.S.A. California: Calistoga, 7 May 1900, *A. Eastwood s.n.* (holotype, UC [barcode] 134569 digital image!; isotype, GH [barcode] 00037694!).

Grindelia hirsutula Hook. & Arn. f. *tomentulosa* Steyerm., Ann. Missouri Bot. Gard. 21: 574. 1934, syn. nov. [described under *Grindelia hirsutula* var. *brevisquama*]. TYPE: U.S.A. California: San Mateo Co., Crystal Springs Lake, 23 June 1913, *W. N. Suksdorf 279* (holotype, MO-850778!).

Grindelia hirsutula Hook. & Arn. var. *calva* Steyerm., Ann. Missouri Bot. Gard. 21: 575. 1934. TYPE: U.S.A. California: San Luis Obispo Co., San Luis Obispo, spring 1905, *J. E. Roadhouse 65* (holotype, UC [barcode] 75916 digital image!).

Grindelia hirsutula Hook. & Arn. var. *subintegra* Steyerm., Ann. Missouri Bot. Gard. 21: 229. 1934. TYPE: U.S.A. California: Ventura Co., 2 mi. E of Ojai, 1 July 1933, *J. T. Howell 11414* (holotype, MO-1044105!; isotypes, CAS [barcode] 00123709 digital image!, CAS [barcode] 00123710 digital image!, F [barcode] 0050286F digital image!, K [barcode] 000250074 digital image!, LL [barcode] 00373592 digital image!, NY [barcode] 00169611 digital image!, US [barcode] 00008207 digital image!).

Grindelia rubricaulis DC. var. *permixta* Steyerm., Ann. Missouri Bot. Gard. 21: 582. 1934, syn. nov. TYPE: U.S.A. California: Alameda Co., San Leandro, 22 July 1929, *J. T. Howell 4352* (holotype, CAS [barcode] 00123675 digital image!).

Perennial subshrubs, 0.35–0.4 m; stems 1 to several, erect, not ramified or with few branches, hirsute to lanuginous. Leaves herbaceous or subcoriaceous, sessile, blade apex acute or obtuse, margin entire or toothed, teeth ending in a sclerotic tip, simple hairs and sessile glandular trichomes present on both blade surfaces; basal leaves narrowly obovate, 9–10 × 1–2 cm, attenuate into a pseudopetiole, blade apex obtuse; cauline leaves oblong to oblong-spatulate, 5–10 × 0.7–2 cm, clasping; blade apex acute or obtuse. Heads radiate, pedunculate, 3.5–4 cm diam.; involucre hemispheric to hemispheric-campanulate, resinous, 9–15 × 20–25 mm; phyllaries in 4 to 8 unequal series, graduated, subulate, with simple hairs and sessile glandular trichomes; the outer bracts narrowly triangular, 5 mm, erect or scarcely reflexed, with few sessile glandular trichomes; the middle bracts narrowly ovate, 7 mm; the upper phyllaries ovate, 10 mm, erect. Ray florets 20 to 48; tube glabrous, ligule narrowly elliptic, 8–15 mm, apex entire, lobed or shortly toothed. Disk florets with corolla 5–6 mm, with a gradually ampliate throat. Achenes dull brown to dark brown, elliptic, 4-angled, 3–4 mm, smooth or striate, apex forming a

crown; pappus of 2 to 4 subulate scales, 3.5–4 mm, somewhat curved, smooth to barbellulate. Chromosome numbers: $2n = 12$ (Raven et al., 1960: 126, sub *G. hirsutula* and *G. rubricaulis* var. *permixta*; Lane, 1993: 272); $2n = 24$ (Lane, 1993: 272).

Iconography. Steyermark (1934: 579, fig. 35); Lane (1993: 279).

Distribution and habitat. *Grindelia hirsutula* grows on sandy and clay soils, in slopes and roadsides, at 900 m, in California (U.S.A).

Phenology. *Grindelia hirsutula* flowers from May to September.

Etymology. The specific epithet is taken from the Latin "hirsutus," meaning "covered by straight ascending trichomes."

Common name. Hairy gumweed (<http://plants.usda.gov/>).

Discussion. *Grindelia hirsutula* is characterized by its radiate heads, 3.5–4 cm diameter, with subulate phyllaries arranged in graduated series. The taxon is related to *G. villarrealii* G. L. Nesom, with which it shares a nonrhizomatous habit and leaves with sessile glandular trichomes not in pits. *Grindelia hirsutula* differs by its larger-sized heads (vs. 1.3–1.5 cm diameter in *G. villarrealii*), the absence of stipitate glandular trichomes, and nontuberculate achenes.

Greene (1883) noted that in the collections at CAS, two different species are included under the name *Grindelia hirsutula*: one a more slender taxon, with smaller heads and shorter phyllaries, and the other stout, with long, spreading phyllaries. Later he described the stout taxon under the name *G. patens*, a species different from *G. hirsutula*, but matching in part the concept of *G. hirsutula* from Gray. Nevertheless, Steyermark (1934) considered *G. patens* a variety of *G. hirsutula*, and Lane (in sched., 1993) considered the type of *G. patens* a hybrid between *G. hirsutula* var. *hirsutula* and *G. stricta* var. *platyphylla* (Greene) M. A. Lane.

The species *Grindelia rubricaulis*, *G. pacifica*, and *G. patens* were established, based on characters with continuous variation within this species.

Four forms were described by Steyermark (1934) within *Grindelia hirsutula* and represent variability within its species concept. Four varieties were further established by Steyermark (1934): three within *G. hirsutula* as variety *brevisquama*, variety *calva*, and variety *subintegra* and a fourth associated with another species as *G. rubricaulis* var. *permixta*. These eight infraspecific names for Steyermark all newly synonymize as no more than variation seen within the species *G. hirsutula*. Similarly, Strother and Wetter (2006) included some 30 names within their synonymy of *G. hirsutula* (including *G. rubricaulis*), some of which are accepted as independent taxonomic species herein, while others synonymize elsewhere in the present paper. In the broad concept of *G. hirsutula* recognized by Strother and Wetter, the taxon has a wide distribution area in Canada and most of the United States.

Additional specimens examined. U.S.A. **California:** Alameda Co., Albany Hills in Albany betw. San Pablo Ave. & Interstate 80, *B. Ertter 10142* (NY); Marin Co., Sausalito, *A. Eastwood 280* (MO); San Bruno Hills, *A. D. E. Elmer 4267* (MO); along railroad N of San Rafael, *J. T. Howell 21491* (MO); Sausalito Hills, *J. T. Howell 11455* (MO), *J. T. Howell 11456* (MO); Sausalito Hills, *J. T. Howell 11457* (MO); White's Hill, betw. Fairfax & Woodacre, *J. T. Howell 11463* (MO); Sausalito Hills, Napa Co., E side of Napa Valley, near Stags Leap, *J. T. Howell 11394* (MO); San Francisco Co., San Luis Obispo, summit of Cuesta Paso, *J. T. Howell 11415* (MO); hills of Visitación Valley, *J. T. Howell 11436* (MO); near San Francisco, 1866, *A. Kellogg s.n.* (MO-130116); San Mateo Co., Spring Valley Lake, *D. Demaree 10424* (MO); San Francisco Bay, *D. Demaree 10523* (MO); above Crystal Springs on Half Moon Bay Rd., *A. A. Heller 8575* (MO); San Andreas Lake, open Clay Hills, *L. S. Rose 33221* (MO); Santa Clara Co., foothills W of Los Gatos, *A. A. Heller 7461* (PH); Sonoma Co., 4 mi. from Santa Rosa on rd. to Sonoma, *J. T. Howell 4304* (MO); 8 mi. W of Petaluma, *J. T. Howell 5223* (MO).

14. Grindelia hirtella (B. L. Rob. & Greenm.) Adr. Bartoli & Tortosa, comb. et stat. nov. Basionym: *Grindelia squarrosa* (Pursh) Dunal var. *hirtella* B. L. Rob. & Greenm., Amer. J. Sci. Arts, ser. 3, 50: 153. 1895. *Grindelia inuloides* Willd. var. *hirtella* (B. L. Rob. & Greenm.) G. L. Nesom, Phytologia 68: 326. 1990. TYPE: Mexico. Oaxaca: Las Sedas, 6000 ft., 16 Aug. 1894, *C. G. Pringle 4805* (holotype, GH [barcode] 00008457 digital image!; isotypes, BKL [barcode] 00000146 digital image!, GOET [barcode] 001588 digital image!, M [barcode] 0029681 digital image!, MEXU-33270 digital image!, MO-130334!, NY [barcode] 169643!, P [barcode] 00742808 digital image!, PH-47868!, TEX [barcode] 00000478 digital image!). Figure 6.

Biannual or perennial subshrubs, 0.15–1 m; stems 1, rarely 2 or more, erect, ramified, pubescent. Leaves subcoriaceous, sessile, oblong, elliptic, or obovate, 2–5 × 1–2 cm, clasping, auriculate; blade apex obtuse, margin entire, crenate, serrate or toothed, teeth ending in a sclerotic tip, simple hairs scattered, sessile glandular trichomes present on both blade surfaces. Heads radiate, pedunculate, 1.5–2 cm diam.; involucre hemispheric to hemispheric-

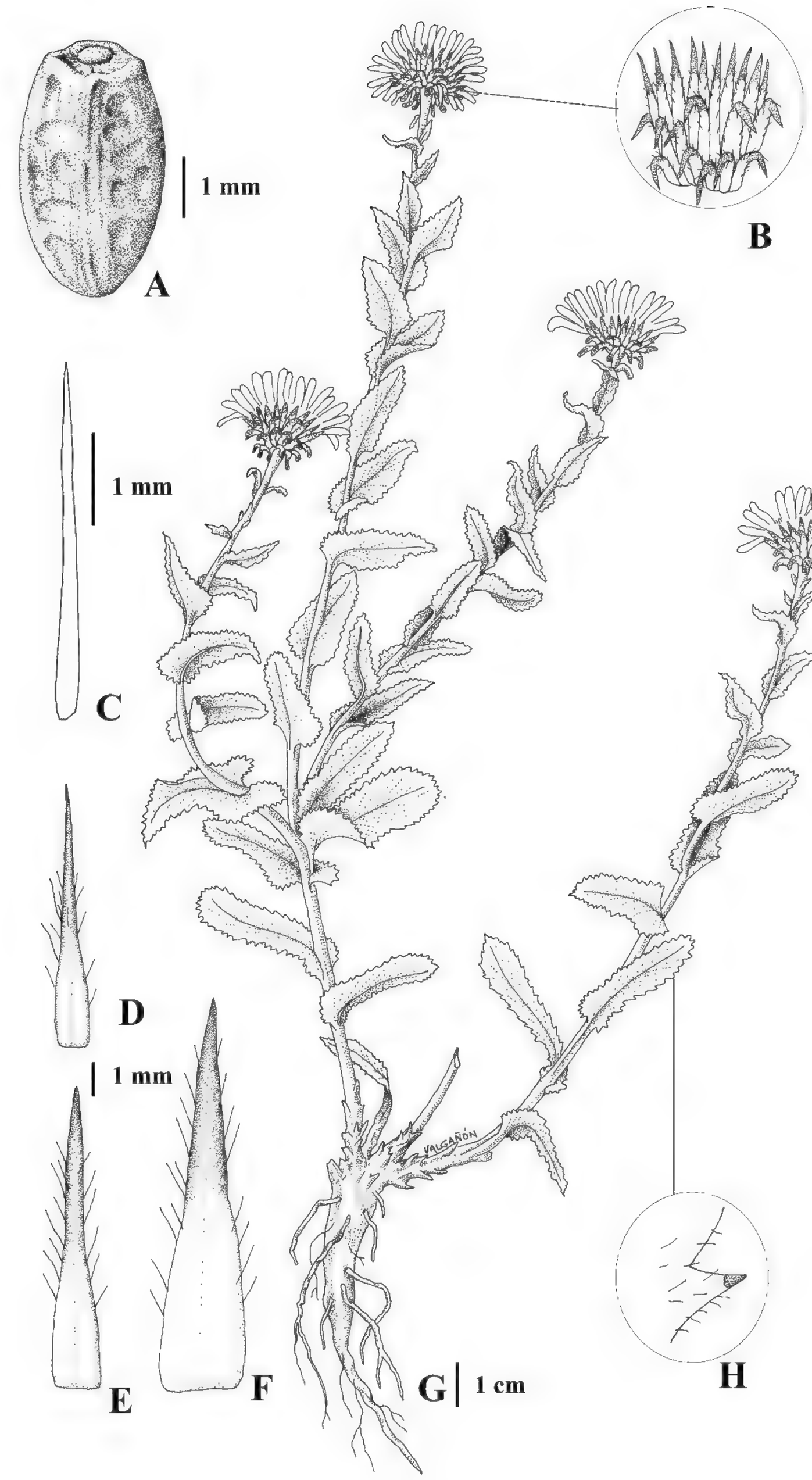

Figure 6. *Grindelia hirtella* (B. L. Rob. & Greenm.) Adr. Bartoli & Tortosa. —A. Achene, showing the tuberculate surface, subquadrate. —B. Involucre, with phyllaries in four to six series. —C. Pappus, showing one of two or three bristles. D–F. Representative phyllaries. —D. Outer series. —E. Middle series. —F. Inner series. —G. Fertile habit. —H. Leaf tooth, ending in a sclerotic tip, with surfaces showing sessile glandular trichomes. Drawn from *C. L. Smith 686* (MO).

campanulate, resinous, 6–10 × 10–28 mm; phyllaries in 4 to 6 unequal series, graduated, acuminate, linear-elliptic to narrowly ovate, 4–12 mm, spreading or reflexed; acumen linear or narrowly triangular, subterete to terete, 4 mm, straight to spreading, with sessile glandular trichomes. Ray florets 20 to 40; tube glabrous, ligule elliptic, 5–11 mm, apex entire or toothed. Disk florets with corolla 4–6 mm, with a gradually ampliate throat. Achenes dull brown, subquadrate, 2–2.5 mm, tuberculate, apex truncate; pappus of 2 or 3 bristles, 3–3.5 mm, smooth. Chromosome number not known.

Distribution and habitat. *Grindelia hirtella* grows on calcareous hillsides, from 1200 to 1800 m, in the states of Oaxaca and Puebla (Mexico).

Phenology. *Grindelia hirtella* flowers from January to September.

Etymology. The specific epithet is taken from the Latin "hirtus," which refers to being covered with long, weak hairs.

Discussion. Diagnostic features of *Grindelia hirtella* include leaves with teeth that end in a sclerotic tip, with sessile glandular trichomes present on both blade surfaces, these trichomes not in pits; spreading or reflexed phyllaries arranged in graduated series, with a phyllary with subterete or terete acumen, and tuberculate achenes. The taxon was originally described as a variety of *G. squarrosa*, but in this species the teeth of the leaves end in a group of sessile glandular trichomes, the glandular trichomes of the epidermis are in pits, and the achenes are not tuberculate. Nesom (1990) considered *Grindelia hirtella* a variety of *G. inuloides*; however *G. hirtella* is distinguished by its phyllaries arranged in unequal series, in contrast to the subequal series in *G. inuloides*; in addition, the heads are smaller (1.5–2 cm diameter vs. 2.5–3 cm diameter) and the achenes are subquadrate and tuberculate (vs. elliptic and slightly flattened, to 3- or 4-angled, smooth or with transverse incisions).

Additional specimens examined. MEXICO. **Oaxaca:** 8 km NE de San Gabriel, *J. González-Martínez 102* (MO); Oaxaca Valley, *C. L. Smith 686* (MO). **Puebla:** vic. of San Luis Tultitlanapa, near Oaxaca, *C. A. Purpus 2514* (MO).

15. Grindelia humilis Hook. & Arn., Bot. Beechey Voy., 147. 1833. TYPE: U.S.A. California: [probably from San Francisco Bay or Monterey Bay; see Gray, Geol. Surv. Calif. Bot. 1: 304. 1876.] s.d., *Botany Beechey Voyage s.n.* (holotype, K [barcode] 250077 digital image!; isotype, UC [barcode] 292621 digital image!).

Perennial shrubs or subshrubs, 0.3–0.6(–1.5) m; stems 1 to several, erect or creeping, not ramified or with few branches, glabrous or hairy. Leaves succulent, sessile; blade apex acute or obtuse, margin entire or toothed, teeth ending in a sclerotic tip, simple hairs occasionally present along the nerves or at the margin, sessile glandular trichomes present on both blade surfaces, superficial or in pits; basal leaves narrowly obovate, 13–19 × 2–3 cm, attenuate into a pseudopetiole; blade apex acute or obtuse; cauline leaves linear to oblong, 5–9 × 0.8–2 cm, clasping, auriculate; blade apex acute. Heads radiate, pedunculate, 3.5–5 cm diam.; involucre hemispheric to hemispheric-campanulate, resinous, 12–20 × 17–30 mm; phyllaries in 4 or 5 subequal series, acuminate, elliptic to narrowly ovate, 8–15 mm, erect or spreading, glabrous or with simple hairs, margin entire; acumen triangular, flat or subterete, as long as the base, with sessile glandular trichomes. Ray florets 20 to 60; tube glabrous, ligule narrowly elliptic, 18–23 mm, apex entire. Disk florets with corolla 5–6 mm, with an abruptly ampliate throat. Achenes elliptic, light brown, 4-angled, 3–5 mm, smooth or rugose, apex truncate or oblique; pappus of 2 to 5 subulate scales, 2.5–3 mm, curved, smooth to barbellulate.

Etymology. The specific epithet is taken from the Latin "humilis" for "low-growing," which refers to the size of the plant.

Discussion. *Grindelia humilis* is characterized by acuminate phyllaries, arranged in subequal, four or five series, with a triangular acumen as long as the phyllary base. The marginal teeth of its leaves end in a sclerotic tip, and the pappus consists of curved, subulate scales. The taxon is related to *G. greenmanii* and *G. inuloides*, sharing leaf teeth that end in a sclerotic tip and phyllaries arranged in subequal series. These two latter taxa differ by the acumen of the phyllaries. The acumen is also triangular but shorter in *G. greenmanii*, less than the basal segment; the acumen is narrower and linear-elliptic to narrowly ovate in *G. inuloides*. Both these species share a pappus of bristles, in contrast to the subulate scales seen in *G. humilis*.

The type specimen for *Grindelia humilis* consists of only the apical portion of the plant and lacks the basal stem and leaves. This may be why Hooker and Arnott described the species as a dwarf herb with narrowly linear and entire leaves.

Lane (1992) and Strother and Wetter (2006) included *Grindelia humilis* as a synonym of *G. hirsutula*, but the latter species differs from *G. humilis* by its subulate phyllaries arranged in graduated series.

Two varieties are recognized for *Grindelia humilis* and can be distinguished by the following couplet.

1a. Stems erect; leaves with apex acute to obtuse, glandular trichomes not in pits ..... 15a. *G. humilis* var. *humilis*

1b. Stems creeping; leaves with apex rounded, glandular trichomes always in pits ..... 15b. *G. humilis* var. *platyphylla*

15a. Grindelia humilis var. **humilis.**

Grindelia stricta DC., Prodr. (DC.) 7: 278. 1838, syn. nov. TYPE: U.S.A. Alaska: Portum Mulgrave, *T. Haenke*

s.n. (holotype, "herb. Haenke" not seen; isotypes, G-DC, IDC microfiche!, UC [barcode] 292722 digital image!).

Grindelia robusta Nutt., Trans. Amer. Philos. Soc., n.s. 7: 314. 1840, syn. nov. *Grindelia rubricaulis* DC. var. *robusta* (Nutt.) Steyerm., Ann. Missouri Bot. Gard. 21: 227. 1934. TYPE: U.S.A. California: San Pedro, *T. Nuttall s.n.* (holotype, PH [barcode] 01085478, p.p. [fertile stem at left]!; isotype, GH [barcode] 00037708!).

Grindelia cuneifolia Nutt., Trans. Amer. Philos. Soc. 7: 315. 1841, syn. nov. *Grindelia robusta* Nutt. var. *angustifolia* A. Gray, Bot. California [W. H. Brewer], 304. 1876, nom. nov. for *Grindelia cuneifolia* Nutt. *Grindelia stricta* DC. var. *angustifolia* (A. Gray) M. A. Lane, Novon 2(3): 217. 1992. TYPE: U.S.A. California: Santa Barbara Co., Santa Barbara, s.d., *T. Nuttall s.n.* (holotype, BM [barcode] 001025306 digital image!; isotype, GH [barcode] 00037687!).

Grindelia latifolia Kellogg, Proc. Calif. Acad. Sci. 5: 36. 1873, syn. nov. *Grindelia robusta* Nutt. var. *latifolia* (Kellogg) Jeps., Man. Fl. Pl. Calif. [Jepson], 1020. 1925. *Grindelia rubricaulis* DC. var. *latifolia* (Kellogg) Steyerm., Ann. Missouri Bot. Gard. 21: 227. 1934. TYPE: U.S.A. California: Santa Barbara Co., Santa Rosa Island, 1872–1873, *W. G. W. Harford s.n.* (holotype, GH [barcode] 00008430!).

Grindelia oregana A. Gray, Syn. Fl. N. Amer. 1(2): 118. 1884, syn. nov. TYPE: U.S.A. Washington: Fidalgo Island, 1838, *D. Lyall s.n.* (holotype, GH [barcode] 00037706!).

Grindelia hendersonii Greene, Pittonia 2: 18. 1889, syn. nov. *Grindelia stricta* DC. var. *hendersoni* (Greene) Steyerm., Ann. Missouri Bot. Gard. 21: 562. 1934. TYPE: U.S.A. Washington: rocky banks of Lummi Island, Bellingham Bay and S shore of the Gulf of Georgia, 5 July 1888, *L. F. Henderson 1676* (holotype, NDG-53594 digital image!; isotype, GH [barcode] 00037691!).

Grindelia lanata Greene, Pittonia 2: 290. 1892, syn. nov. *Grindelia stricta* DC. var. *lanata* (Greene) Steyerm., Ann. Missouri Bot. Gard. 21: 563. 1934. TYPE: Canada. British Columbia: Oak Bay, Vancouver Island, 18 June 1887, *J. Macoun s.n.* (holotype, NDG-53607 digital image!; isotype, BM [barcode] 001025307 digital image!).

Grindelia paludosa Greene, Man. Bot. San Francisco 172: 1894, syn. nov. *Grindelia cuneifolia* (Nutt.) var. *paludosa* (Greene) Jeps., Fl. W. Calif. [Jepson], 556. 1901. TYPE: U.S.A. California: Suisun Marsh, 29 Sep. 1889, *E. L. Greene s.n.* (holotype, NDG-53622 digital image!; isotype, NY [barcode] 00008410!).

Grindelia macrophylla Greene, Pittonia 3: 297. 1898, syn. nov. *Grindelia stricta* DC. var. *macrophylla* (Greene) Steyerm., Ann. Missouri Bot. Gard. 21(3): 561. 1934. *Grindelia integrifolia* DC. var. *macrophylla* (Greene) Cronquist, Vasc. Pl. Pacific NorthW. [C. L. Hitchcock & al.] 5: 207. 1955. TYPE: Canada. British Columbia: Vancouver, July 1890, *E. L. Greene s.n.* (holotype, NDG-53613 digital image!; isotype, NDG-53614 digital image!).

Grindelia robusta Nutt. var. *davyi* Jeps., Fl. W. Calif. [Jepson], 554. 1901, as "Davyi," syn. nov. *Grindelia camporum* Greene var. *davyi* (Jeps.) Steyerm., Ann. Missouri Bot. Gard. 21: 534. 1934. *Grindelia hirsutula* Hook. & Arn. var. *davyi* (Jeps.) M. A. Lane, Novon 2(3): 216. 1992. TYPE: U.S.A. California: Berkeley, Peralta Park, 10 June 1896, *J. Burtt Davy s.n.* (holotype, JEPS [barcode] 21750 digital image!; isotypes, UC [barcode] 32128 digital image!, UC [barcode] 32135 digital image!).

Grindelia integrifolia DC. var. *aestivalis* J. K. Henry, Fl. S. Brit. Columbia, 291. 1915, syn. nov. TYPE: Canada. British Columbia: near shore, Oak Bay, Victoria, 26 July 1913, *J. K. Henry s.n.* (holotype, NY [barcode] 00169607!).

Grindelia integrifolia DC. var. *autumnalis* J. K. Henry, Fl. S. Brit. Columbia, 291. 1915, syn. nov. TYPE: Canada. British Columbia: Victoria, Vancouver Island, 7 July 1913, *J. K. Henry s.n.* (holotype, CAS [barcode] 00123714 digital image!; isotype, CAS [barcode] 00123715 digital image!).

Grindelia collina J. K. Henry, Fl. S. Brit. Columbia, 291. 1915, syn. nov. *Grindelia stricta* DC. var. *collina* (J. K. Henry) Steyerm., Ann. Missouri Bot. Gard. 21: 564. 1934. TYPE: Canada. British Columbia: dry hill, Thetis Lake, near Victoria, Vancouver Island, 18 July 1915, *J. K. Henry s.n.* (holotype, NY [barcode] 169600!; isotype, CAS [barcode] 00123702 digital image!).

Grindelia oregana A. Gray subsp. *wilkesiana* Piper, Fl. N.W. Coast [Piper & Beattie], 363. 1915, syn. nov. TYPE: U.S.A. Washington: Gray's Harbor Co., betw. Gray's Harbor & Satchap River, *Wilkes Expedition s.n.* (holotype, NY [barcode] 8408!).

Grindelia andersonii Piper, Proc. Biol. Soc. Wash. 31: 77. 1918, syn. nov. *Grindelia stricta* DC. var. *andersonii* (Piper) Steyerm., Ann. Missouri Bot. Gard. 21: 559. 1934. TYPE: Canada. British Columbia: Saanich Arm, Vancouver Island, 5 July 1917, *G. R. Anderson s.n.* (holotype, US [barcode] 00008202 digital image!).

Grindelia rubricaulis DC. var. *interioris* Jeps., Man. Fl. Pl. Calif. [Jepson], 1021, syn. nov. *Grindelia camporum* Greene var. *interioris* (Jeps.) Steyerm., Ann. Missouri Bot. Gard. 21: 538. 1934. TYPE: U.S.A. California: Calaveras Co., Copperopolis, Mokelumne Hill, 18–30 May 1895, *J. Burtt Davy 1383* (holotype, UC [barcode] 32130 digital image!).

Grindelia aggregata Steyerm., Ann. Missouri Bot. Gard. 21: 566. 1934, syn. nov. TYPE: Canada. British Columbia: Victoria, 27 Aug. 1903, *J. W. Congdon s.n.* (holotype, MO [barcode] 714911!).

Grindelia camporum Greene f. *foliacea* Steyerm., Ann. Missouri Bot. Gard. 21: 534. 1934, syn. nov. [described under *Grindelia camporum* var. *interioris*]. TYPE: U.S.A. California: Solano Co., clay hill, 1 mi. from Vacaville on rd. to Elmira, 30 May 1930, *J. T. Howell 5201* (holotype, CAS [barcode] 00123703 digital image!; isotype, GH [barcode] 00037685!).

Grindelia humilis Hook. & Arn. f. *pubescens* Steyerm., Ann. Missouri Bot. Gard. 21: 527. 1934, syn. nov. TYPE: U.S.A. California: Napa Co., upper edge of tidal flat, Cuttings Wharf, on Napa River, 8 Oct. 1932, *J. T. Howell 10805* (holotype, CAS [barcode] 00123711 digital image!; isotypes, GH [barcode] 00037685!, MO [barcode] 714095!).

Grindelia humilis Hook. & Arn. f. *reflexa* Steyerm., Ann. Missouri Bot. Gard. 21: 526. 1934, syn. nov. TYPE: U.S.A. California: Oakland, salt marsh, 15 Nov. 1883, *E. L. Greene s.n.* (holotype, GH [barcode] 00037699!).

Grindelia stricta DC. var. *aestuarina* Steyerm., Ann. Missouri Bot. Gard. 21: 560. 1934, syn. nov. TYPE: U.S.A. Washington: tide lands, Marysville, June 1928,

J. M. Grant s.n. (holotype, RM [barcode] 0001129 digital image!).

Grindelia stricta DC. f. *elongata* Steyerm., Ann. Missouri Bot. Gard. 21: 560. 1934, syn. nov. [described under *Grindelia stricta* var. *aestuarina*]. TYPE: Canada. British Columbia: margin of arm of Victoria Harbor, 3 mi. from Victoria on Island hwy., Vancouver Island, 27 July 1931, *J. T. Howell 7545* (holotype, CAS [barcode] 00123677 digital image!; isotypes, CAS [barcode] 188501 digital image!, MO [barcode] 714912!).

Grindelia blackei Steyerm., Ann. Missouri Bot. Gard. 21: 567. 1934, syn. nov. *Grindelia stricta* DC. subsp. *blakei* (Steyerm.) D. D. Keck, Aliso 4: 102. 1958. TYPE: U.S.A. California: Humboldt Co., Eureka, salt meadows along canal, 9 Aug. 1931, *J. A. Moore & J. A. Steyermark 3686* (holotype, MO [barcode] 714076!; isotypes, MO [barcode] 714091!, UC [barcode] 520410 digital image!).

Stems erect. Leaves with apex acute to obtuse, blade with few sessile glandular trichomes. Chromosome numbers: $2n = 12$ (Raven et al., 1960: 126, sub *Grindelia rubricaulis* var. *robusta*; Pinkava & Keil, 1977: 681, sub *G. latifolia*; Lane, 1993: 274, sub *G. stricta* var. *angustifolia*; Lane & Li, 1993: 542, sub *G. hirsutula* var. *davyi*, *G. stricta* var. *stricta*, *G. stricta* var. *angustifolia*; Semple et al., 1989: 302, sub *G. stricta*; Chambers et al., 1998: 19, sub *G. stricta*); $2n = 24$ (Lane, 1993: 274, sub *G. stricta* var. *angustifolia*).

Iconography. Lane (1993: 279), sub nom *Grindelia stricta*.

Distribution and habitat. *Grindelia humilis* var. *humilis* grows along seashores, sand dunes, and lowlands, from 0 to 200 m, from southern Alaska (U.S.A.) and southwestern Canada to California (U.S.A).

Phenology. *Grindelia humilis* var. *humilis* flowers from May to November.

Common name. Oregon gumweed (<http://plants.usda.gov/>, sub nom. *Grindelia stricta* var. *platyphylla*).

Discussion. The high variation in the shape of leaves and in the general pubescence of the plants for *Grindelia humilis* accounts for the significant number of synonyms. The types of *G. robusta* and *G. stricta* share diagnostic characters with *G. humilis* var. *humilis*, including erect stems, leaves with marginal teeth that end in a sclerotic tip, and pedunculate heads with phyllaries with an acuminate involucre, arranged in subequal series, with a triangular acumen as long as the phyllary base. In the case of Nuttall's species *G. cuneifolia*, the type seems to be an abnormal specimen with sessile heads (see Steyermark, 1934: 593). The name *cuneifolia* was replaced by Gray with the varietal name *angustifolia* under *G. robusta*.

Most of the synonyms for *Grindelia humilis* and included here were previously considered at lower rank by Steyermark (1934), as varieties of *G. camporum*, *G. rubricaulis* (this species refers to *G. hirsutula* in the current paper), or *G. stricta* (referred to *G. humilis* herein). *Grindelia humilis* and several other names (*G. blackei*, *G. macrophylla*, *G. paludosa*, *G. robusta*, *G. robusta* var. *davyi*, and *G. stricta*) were relegated to the synonymy of *G. hirsutula* by Strother and Wetter (2006). Nevertheless, the taxon recognized herein as *G. humilis* can be distinguished from *G. camporum* by its phyllaries in subequal series, a triangular acumen (vs. a graduated phyllary series with a terete or subterete acumen in *G. camporum*); the corolla of disk florets with an abruptly ampliate throat (vs. gradually ampliate); and the achenes elliptic, 4-angled (vs. broadly elliptic and 2- or 3-angled). In *G. hirsutula*, the phyllaries are subulate and arranged in graduated series, and the corolla of disk florets presents a gradually ampliate throat.

Lane (1992) considered the type of *Grindelia robusta* to be a hybrid between *G. hirsutula* var. *hirsutula* and a variety of *G. stricta*. The type of *G. camporum* f. *foliacea* (Lane, in sched.) was annotated as a hybrid between *G. hirsutula* var. *davyi* and *G. hirsutula* var. *hirsutula*, that of *G. humilis* var. *pubescens* (Lane, in sched.) a hybrid between *G. camporum* var. *camporum* and *G. stricta* var. *angustifolia*, that of *G. latifolia* (Lane, in sched.) a hybrid between *G. camporum* var. *bracteosa* (J. T. Howell) M. A. Lane and *G. stricta* var. *platyphylla* [= *G. humilis* var. *platyphylla* herein], that of *G. paludosa* (Lane, in sched., NY and UC) a hybrid from *G. camporum* var. *camporum* × *G. stricta* var. *angustifolia*, *G. robusta* (Lane, in sched., GH) a hybrid from *G. hirsutula* var. *hirsutula* × *G. stricta* var. *platyphylla*, and finally that of *G. hirsutula* var. *davyi* may be a possible derivative of *G. hirsutula* var. *hirsutula* × *G. camporum* (Lane, 1993).

Additional specimens examined. CANADA. **British Columbia:** Vancouver Island, vic. of Victoria, *J. Macoun 420* (MO); Kitsap Co., Keyport, *W. J. Eyerdam 1179* (GH); Skagit Co., Rosario Beach, *W. J. Eyerdam 1302* (GH); strait of Juan de Fuca, near Victoria, Vancouver Island, *R. C. Rollins & T. S. Chambers 2691* (GH); Sidney, Vancouver Island, *T. M. C. Taylor 3009* (GH). U.S.A. **California:** Amador Co., *G. Hansen 172* (MO), *G. Hansen 1672* (MO); Butte Co., Little Chico Creek, *R. M. A. 725* (MO-130117); Table Mtn., olive ranch, N of Oroville, *A. A. Heller 10780* (MO); E side of turn off upper Bidwell Park to Bear Hole, *D. Isle 478* (MO); Plumas Natl. Forest on state rd. 23N06, 1.5 mi. N of jct. with hwy. 70, *H. H. Schmidt, M. Merello & L. Woodruff 864* (MO); Calaveras Co., Jenny Lind, dry hillside, *E. E. Stanford 969* (MO); Contra Costa Co., tidal flat at mouth of Rodeo Creek, 8 Oct. 1932, *J. T. Howell 10796*

(MO); Humboldt Co., salt marsh at Eureka, *A. A. Heller 1840* (MO); along hwy. near crossing of Eel River, S of Garberville, *A. A. Heller 13764* (MO); NW of Eureka on W side of Arcata Bay, just N of CA state hwy. 255 bridge on Samoa Peninsula along Vance Ave., *M. A. Lane 3138* (MO); Kings Co., Fort Lawton, edge of saltwater marsh, 25 July 1937, *W. J. Eyerdam s.n.* (MO-1158524); Lincoln Co., Sacramento Valley, 1 mi. NW of Placer, *C. B. Wolf 8619* (MO); Marin Co., sandy flats, Point Reyes Peninsula, *J. T. Howell 11710* (MO); Mt. Tamalpais, dry slopes, *L. S. Rose 33315* (MO); Mendocino Co., bluff 1 mi. N of Fort Bragg, 10 Aug. 1938, *A. A. Heller s.n.* (MO-1162225); Napa Co., Mt. St. Helena, *J. T. Howell 5346* (MO); Nevada Co., near Nevada city, *A. A. Heller 8117* (MO); San Francisco, vic. of Berkeley, *H. A. Walker 430* (PH); San Mateo Co., S San Francisco, *J. A. Moore & J. A. Steyermark 3684* (MO); Santa Clara Co., Alviso, *E. B. Bartram s.n.* (PH), 17 Aug. 1906, *C. S. Williamson s.n.* (PH); Solano Co., Suisun Marsh along railroad near Suisun, *A. A. Heller 7542* (MO), 29 Sep. 1889, *E. L. Greene s.n.* (MO-738819); salt marsh at Suisun, *J. T. Howell 11723* (MO); Tubbs Island, *H. E. Parks & S. T. Parks 0411* (MO, PH); Suisun, *L. S. Rose 33367* (MO); Sonoma Co., marsh W of creek N of Santa Rosa, *A. A. Heller 5810* (MO); The Geysers, *E. Marcus &. A. M. Jones 29142* (MO); Sonoma, *L. S. Rose 40364* (MO); Tuolumne Co., Sierra Nevada, along rd. from Twain Harte to Sonora, *A. M. Alexander & L. Kellogg 3712* (MO); Yolo Co., near Madison, *A. A. Heller & H. E. Brown 5578* (MO). **Oregon:** Lane Co., Florence, *L. F. Henderson 13987* (PH); lagoon shores at mouth of Siuslaw River, 7 Sep. 1911, *Gorman s.n.* (PH); Tillamook Co., Tillamook Bay, *L. F. Henderson 433* (MO), Garibaldi, *M. E. Peck 13359* (PH); **Washington:** Clallam Co., Mora, sea beach, *G. N. Jones 3442* (MO); Clallam Co., Port Angeles, *J. W. Thompson 7855* (MO, PH); King Co., Seattle, July 1915, *G. N. Friberg s.n.* (MO-813677); Seattle, on beach, 24 Sep. 1934, *G. N. Jones s.n.* (MO-1251042); Seattle, Sep. 1929, *G. B. Rigg s.n.* (MO-979122); Seattle, Oct. 1910, *S. M. Zeller s.n.* (MO-813515); Argyle, San Juan Island, *S. M. Zeller & E. B. Zeller 956* (MO); Kitsap Co., Manitou Beach, on back beach, *W. J. Eyerdam 1150* (MO); Pierce Co., shores of Puget Sound near Steilacoom, *J. W. Thompson 9959* (MO); San Juan Co., Orcas Island, 4 July 1935, *W. J. Eyerdam s.n.* (MO-1153051); beach Three Tree Point, near Seattle, 23 Sep. 1937, *G. N. Jones s.n.* (MO-1251044); Skagit Co., *J. W. Thompson 10091* (MO); Thurston Co., salt marsh bordering head of Mud Bay, ca. 5 mi. W of Olympia, *F. G. Meyer 1588* (MO, PH).

15b. Grindelia humilis var. **platyphylla** (Greene) Adr. Bartoli & Tortosa, comb. nov. Basionym: *Grindelia robusta* Nutt. var. *platyphylla* Greene, Pittonia 2: 289. 1892. *Grindelia rubricaulis* DC. var. *platyphylla* (Greene) Steyerm., Ann. Missouri Bot. Gard. 21: 227. 1934. *Grindelia latifolia* Kellogg subsp. *platyphylla* (Greene) D. D. Keck, Aliso 4: 102. 1958. *Grindelia stricta* DC. var. *platyphylla* (Greene) M. A. Lane, Novon 2: 217. 1992. TYPE: U.S.A. California: Monterey Co., Pacific Grove, July 1892, *M. A. Howe s.n.* (lectotype, designated by Lane [1992: 217], UC [barcode] 32131 digital image!; isolectotype, UC [barcode] 32132 [locality only as "Monterey"] digital image!).

Grindelia rubricaulis DC. var. *maritima* Greene, Pittonia 2: 289. 1892, syn. nov. *Grindelia robusta* Nutt. var. *maritima* (Greene) Jeps., Fl. W. Calif. [Jepson], 554. 1901. *Grindelia maritima* (Greene) Steyerm., Ann. Missouri Bot. Gard. 21: 576. 1934. *Grindelia hirsutula* Hook. & Arn. var. *maritima* (Greene) M. A. Lane, Novon 2: 216. 1992. TYPE: U.S.A. California: Point Lobos, 12 Aug. 1892, *E. L. Greene s.n.* (holotype, NDG 53637 digital image!; isotype, UC [barcode] 32144 digital image!).

Grindelia venulosa Jeps., Man. Fl. Pl. Calif. [Jepson], 1021. 1925, syn. nov. *Grindelia stricta* DC. f. *venulosa* (Jeps.) Steyerm., Ann. Missouri Bot. Gard. 21: 558. 1934. *Grindelia stricta* DC. subsp. *venulosa* (Jeps.) D. D. Keck, Aliso 4: 102. 1958. TYPE: U.S.A. California: Humboldt Co., in quicksand on seashore near Big Flat, 1867, *H. N. Bolander 6493* (holotype, JEPS [barcode] 2620 digital image!; isotype, US [barcode] 00323468 digital image!).

Grindelia arenicola Steyerm., Ann. Missouri Bot. Gard. 21: 229. 1934, syn. nov. TYPE: U.S.A. California: Mendocino Co., Mendocino coastal plain, 4.5 mi. N of Ft. Bragg, 14 Sep. 1930, *J. T. Howell 5473* (holotype, CAS [barcode] 00123698 digital image!, xerox at BAA!; isotypes, GH [barcode] 00037683!, UC [barcode] 473548 digital image!).

Grindelia arenicola Steyerm. var. *pachyphylla* Steyerm., Ann. Missouri Bot. Gard. 21: 596. 1934, syn. nov. TYPE: U.S.A. California, Mendocino Co., open coastal plain, 6 mi. S of Point Arena, 27 Sep. 1931, *J. T. Howell 8106* (holotype, CAS [barcode] 00123699 digital image!; isotypes, GH [barcode] 00037684!, MO [barcode] 714075!).

Grindelia arenicola Steyerm. f. *trichophora* Steyerm., Ann. Missouri Bot. Gard. 21: 596. 1934, syn. nov. [described under *Grindelia arenicola* var. *pachyphylla*]. TYPE: U.S.A. California: San Mateo Co., Half-moon Bay, 1913, *W. F. Schmitt s.n.* (holotype, US [barcode] 00008203 digital image!).

Grindelia maritima (Greene) Steyerm. f. *anomala* Steyerm., Ann. Missouri Bot. Gard. 21: 578. 1934, syn. nov. TYPE: U.S.A. California: Laguna Honda, San Francisco, 15 Sep. 1933, *J. T. Howell 11658* (holotype, MO-1044116!; isotype, CAS [barcode] 205557 digital image!).

Grindelia rubricaulis DC. f. *pubescens* Steyerm., Ann. Missouri Bot. Gard. 21: 589. 1934, syn. nov. [described under *Grindelia rubricaulis* var. *latifolia*]. TYPE: U.S.A. California: Monterey Co., betw. Lucia & Little Hot Springs, 14 June 1909, *K. Brandegee s.n.* (holotype, UC [barcode] 468770 digital image!; isotypes, CAS [barcode] 00123674 digital image!, CAS [barcode] 237886 xerox!).

Grindelia rubricaulis DC. f. *minor* Steyerm., Ann. Missouri Bot. Gard. 21: 589. 1934, syn. nov. [described under *Grindelia rubricaulis* var. *latifolia*]. TYPE: U.S.A. California: Santa Barbara Co., Casmailia sands, country adjacent to Santa Maria, 13 June–3 July 1906, *A. Eastwood 794* (holotype, GH [barcode] 00037711!; isotypes, CAS [barcode] 00123673 digital image!, US [barcode] 00008214 digital image!).

Grindelia rubricaulis DC. f. *villosa* Steyerm., Ann. Missouri Bot. Gard. 21: 590. 1934, syn. nov. [described under *Grindelia rubricaulis* var. *platyphylla*]. TYPE: U.S.A. California: Monterey Co., Pacific Grove, coast above Chinatown Point, 10 July 1905, *C. P. Smith 1016*

(holotype, GH [barcode] 00037712!; isotypes, MICH [barcode] 1107423 digital image!, US [barcode] 00344741 digital image!).

Grindelia stricta DC. var. *procumbens* Steyerm., Ann. Missouri Bot. Gard. 21: 559. 1934, syn. nov. TYPE: U.S.A. California: Humboldt Co., on sandy seashore at base of cliffs, 10 mi. N of Trinidad, 9 Aug. 1931, *J. A. Moore & J. A. Steyermark 3687* (holotype, MO [barcode] 714077!; isotype, MO [barcode] 714078!).

Stems creeping. Leaves with apex rounded; sessile glandular trichomes always in pits. Chromosome numbers: $2n = 12$ [Raven et al., 1960: 126, sub *Grindelia arenicola*, *G. maritima*; Pinkava & Keil, 1977: 681, sub *G. latifolia* subsp. *platyphylla*]; $2n = 24$ (Lane, 1993: 274, sub *G. stricta* var. *platyphylla*).

Iconography. Lane (1993: 279), sub *Grindelia stricta* var. *platyphylla*.

Distribution and habitat. *Grindelia humilis* var. *platyphylla* has been collected on sand dunes and coastal bluffs, from 0 to 200 m, in California (U.S.A).

Phenology. *Grindelia humilis* var. *platyphylla* has been collected in flower from the beginning of July to October.

Etymology. The name of this variety was taken from the Greek "platy-," meaning "broad," and "-phyllum," meaning "leaf," which refers to the shape of the leaves.

Discussion. Both varities considered here have broad leaves (up to 2 cm wide).

Grindelia venulosa was merged in *G. stricta* (= *G. humilis* var. *humilis* in the present paper) by both Steyermark (1934) and Lane (1992), and was later considered a synonym of *G. hirsutula* by Strother and Wetter (2006). Lane also considered Steyermark's coastal species *G. arenicola* within the variation associated with *G. humilis* var. *platyphylla*, but she associated the variety with *G. stricta* rather than *G. humilis*. In contrast to its synonymy here, Steyermark's species *G. maritima* was included in *G. hirsutula* by both Lane (1992) and Strother and Wetter (2006). Greene (1892: 289) originally distinguished *G. rubricaulis* var. *maritima* by the pubescence and red stems of the plants. He distinguished two varieties for *Grindelia*, both along the Californian coast, and both varieties synonymize within the variability seen for *G. humilis* var. *platyphylla*. The phyllaries of *G. humilis* are subequal and acuminate, differing from those of *G. hirsutula*, which appear in a graduated series on the involucre, with subulate tips. In *G. humilis* var. *platyphylla*, the leaves present glandular trichomes in pits; leaves are not in pits in *G. hirsutula*.

Additional specimens examined. U.S.A. **California:** Humboldt Co., Big Lagoon, *H. E. Parks 24190* (PH); Big Lagoon Park just W of US 101, *P. Wilder 4375* (PH); Monterey Co., *D. Demaree 9235a* (MO); Moss Landing dock area near Marine Lab betw. ocean & hwy. 1, *M. S. Taylor & E. Taylor 5189* (MO); San Luis Obispo Co., San Simeon Bay, *E. Palmer 248* (PH); San Mateo Co., Pigeon Point, slopes by sea, *D. D. Keck 2943* (MO); exposed slope near sea, Fort Winfield Scott, *J. A. Moore & J. A. Steyermark 3685* (MO), 29 Aug. 1909, *W. A. Setchell s.n.* (MO), 21 Oct. 1936, *s. coll.* (PH); Santa Cruz Co., clay soil, 1/4 mi. back from ocean, 6 mi. N of Santa Cruz, *J. T. Howell 10861* (MO).

16. Grindelia integrifolia DC., Prodr. (DC.) 5: 315. 1836. TYPE: U.S.A. Ex America Borealis p. occ. Hort. Soc. Hortic. London, Aug. 1830, *A. de Candolle s.n.* (holotype, G-DC, IDC microfiche!; isotypes, CAS [barcode] 00123713 digital image! [holotype fragm. and photo], GH [barcode] 00037700!, P [barcode] 00742800 digital image!, UC [barcode] 292719 digital image!).

Perennial subshrubs, 0.5–0.8 m, with xylopodium; stem 1, erect, ramified, with stipitate glandular trichomes, simple hairs present or lacking. Leaves herbaceous, sessile, ovate-elliptic, 2–8 × 0.7–3 cm, clasping or base subcordate; blade apex acute or acuminate, margin entire, serrate, denticulate or coarsely dentate, teeth ending in a sclerotic tip, stipitate glandular trichomes on both blade surfaces, sometimes with sessile glandular trichomes in pits. Heads radiate, sessile, 2.5–3 cm diam.; involucre hemispheric, resinous, 5–12 × 12–20 mm; phyllaries in 5 or 6 unequal series, graduated, acuminate, 5–12 mm, erect or spreading, glabrous; acumen filiform, flat, 2–3 mm, erect or lightly spreading, with stipitate or sessile glandular trichomes. Ray florets 16 to 35; tube glabrous, ligule linear-elliptic, 8–15 mm, apex entire. Disk florets with corolla 5–6 mm, with an abruptly ampliate throat. Achenes elliptic, yellowish or dull brownish, 4-angled, 3–4.5 mm, smooth or faintly striate, apex coronate to knobby; pappus of 2 or 3 bristles, 3–4 mm, contorted to curved, smooth to barbellulate.

Etymology. The specific epithet refers to the entire margin of the leaves, from the Latin "integri-," meaning "entire," and "-folius," meaning "-leaved."

Discussion. *Grindelia integrifolia* is characterized by its sessile heads, acuminate phyllaries in graduated series, with filiform acumen, and leaves clasping or with a subcordate base, with stipitate glandular trichomes on both surfaces, the teeth ending in a sclerotic tip.

Two forms are recognized for *Grindelia integrifolia* and may be distinguished by the following couplet.

1a. Leaves with margin entire, occasionally serrate or denticulate, with only stipitate glandular trichomes on both surfaces ..... 16a. *G. integrifolia* f. *integrifolia*

1b. Leaves with margin coarsely dentate, with stipitate glandular trichomes and sessile glandular trichomes in pits on both surfaces ..... 16b. *G. integrifolia* f. *dentata*

16a. Grindelia integrifolia f. **integrifolia.**

Grindelia virgata Nutt., Trans. Amer. Philos. Soc. 7: 314. 1841. *Grindelia integrifolia* DC. var. *virgata* (Nutt.) Torr. & A. Gray, Fl. N. Amer. (Torr. & A. Gray) 2: 248. 1842, non *Grindelia integrifolia* DC. var. *virgata* (Nutt.) Steyerm., Ann. Missouri Bot. Gard. 21: 552–553, nom. illeg. TYPE: U.S.A. Oregon: near Fort Vancouver, s.d., *J. T. Nuttall s.n.* (holotype, PH [barcode] 00047870 digital image!; isotypes, BM [barcode] 000810697 digital image!, PH [barcode] 01085479 digital image!).

Grindelia integrifolia DC. f. *villosa* Steyerm., Ann. Missouri Bot. Gard. 21: 553. 1934, syn. nov. [described under *Grindelia integrifolia* var. *virgata*]. TYPE: U.S.A. Oregon: 1871, *E. Hall 266* (holotype, MO [barcode] 714090!; isotypes, F [barcode] 0050289F digital image!, GH [barcode] 00037701!, MO [barcode] 714092!, NY [barcode] 169608!, US [barcode] 00008210 digital image!).

Leaves with margin entire, occasionally serrate or denticulate, with only stipitate glandular trichomes on both surfaces. Chromosome numbers: $n = 6$ (Chambers et al., 1998: 19, sub *Grindelia integrifolia* × *G. nana*); $2n = 24$ (Morton, 1981: 361).

Iconography. Steyermark (1934: 540, fig. 31).

Distribution and habitat. *Grindelia integrifolia* f. *integrifolia* has been collected in prairies, trenches, and marshy ground, from 0 to 200 m, in Oregon and Washington (U.S.A.).

Phenology. *Grindelia integrifolia* f. *integrifolia* flowers from July to October.

Common name. Puget Sound gumweed (<http://plants.usda.gov/>).

Additional specimens examined. U.S.A. **Oregon:** Hood River Co., *L. F. Henderson 432* (MO), *L. F. Henderson 434* (MO, NY); N Yamhill, 8 July 1882, *J. T. Howell s.n.* (MO, NY); Tillamook Co., Tillamook Bay, 16 July 1882, *L. F. Henderson s.n.* (NY); Washington Co., Twisp, *A. Bradley 477* (MO); vic. Victoria, *J. Macoun 421* (MO). **Washington:** Mason Co., Potlatch St. Park, *A. Colwell & A. Denton 85* (MO).

16b. Grindelia integrifolia f. **dentata** Steyerm., Ann. Missouri Bot. Gard. 21: 551. 1934. TYPE: U.S.A. Oregon: on waste ground, Salem, 14 July 1917, *J. C. Nelson 1670* (holotype, GH [barcode] 00037700!).

Leaves with margin coarsely dentate, with stipitate glandular trichomes and sessile glandular trichomes in pits on both surfaces. Chromosome number not known.

Distribution and habitat. *Grindelia integrifolia* f. *dentata* has been collected on waste ground in Oregon (U.S.A). It is known only from the type specimen, which is a unicate.

Phenology. *Grindelia integrifolia* f. *dentata* flowers in July.

Etymology. The name of this form is taken from the Latin "dentatus," meaning "toothed," which refers to the margin of leaves.

Discussion. *Grindelia integrifolia* f. *dentata* is only known from the type collection, and until further collections from the region are available, we consider it cautious to maintain the taxonomic form.

17. Grindelia inuloides Willd., Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 1: 261. 1807. TYPE: Mexico: cultivated in B, sub nom. *Aster spathulatus* Lindl. (non *Aster spathulatus* Lag.) (lectotype, designated here from B-W-16437 holotype† fragm. at UC, not seen, UC [barcode] 292697 image!).

Perennial subshrubs, 0.2–0.35 m, with xylopodium; stems 1 to several, not ramified or with few branches, glabrous or with stipitate or sessile glandular trichomes. Leaves herbaceous or subcoriaceous, sessile, linear-oblong to oblong, 0.5–6 × 0.2–2 cm, clasping or with base subcordate; blade apex acute, margin subentire or serrate, teeth ending in a sclerotic tip, simple hairs and stipitate or sessile glandular trichomes on both blade surfaces; cauline leaves acuminate, progressively smaller. Heads radiate, subsessile or pedunculate, 2.5–3 cm diam.; involucre hemispheric-campanulate, scarcely resinous, 8–12 × 13–25 mm; phyllaries in 5 or 6 subequal series, acuminate, linear to narrowly oblong, erect or reflexed, 3.5–10 mm, subcoriaceous, with stipitate or sessile glandular trichomes, margin entire; acumen linear-elliptic to narrowly ovate, flat to subterete, ca. 1 mm, with sessile glandular trichomes. Ray florets 25 to 50; tube glabrous, ligule elliptic, 11–16 mm, apex entire. Disk florets with corolla 5–6 mm with a gradually ampliate throat. Achenes dull brown, elliptic, slightly flattened to 3- or 4-angled, smooth or with transverse incisions, apex truncate; pappus of 2 bristles, 3–6.5 mm, smooth.

Etymology. The specific epithet is taken from the genus *Inula* L. (Asteraceae) and, according to the author, refers to its resemblance to this genus.

Discussion. Diagnostic features of *Grindelia inuloides* include the radiate heads with acuminate phyllaries in subequal series within the involucre, the linear-elliptic to narrowly ovate acumen, and the leaves with teeth that end in a sclerotic tip.

Sessé and Mociño collected seeds of *Grindelia inuloides* in Mexico, and in 1804 sent them to the Royal Botanical Garden of Madrid where they were cultivated under the name *Aster spathulatus*. Offspring of these plants were cultivated at Montpellier Botanical Garden. In 1806, Professor P. M. A. Broussonet sent seeds of this species to several botanical gardens, including the Botanic Garden at Berlin, where Willdenow studied the plants cultivated there and described them as a new genus under the name *G. inuloides*.

From 1790 to 1792, Sessé and Mociño's expedition took them from Sonora to Michoacán and then through Álamos and Tarahumara to Aguascalientes (<http://www.rjb.csic.es/jardinbotanico/jardin/index.php?len=&Pag=91>). Comparing the travel of the expedition with the area of distribution of *Grindelia inuloides*, it is probable that the seeds of this taxon were collected in the states of Jalisco or Michoacán.

The type specimen of *Grindelia inuloides* was destroyed during World War II, but its fragment (and a photograph) were conserved at UC, which we propose here as the lectotype of the species. No other isotypes were found in other herbaria.

Three varieties are recognized with *Grindelia inuloides* and may be distinguished by this brief key.

1a. Stems, leaves, and phyllaries with sessile glandular trichomes ..... 17a. *G. inuloides* var. *inuloides*
1b. Stems, leaves, and phyllaries with stipitate glandular trichomes.
  2a. Cauline leaves 0.2–1.5 cm wide .... 17b. *G. inuloides* var. *glandulosa*
  2b. Cauline leaves 2 cm wide .... 17c. *G. inuloides* var. *latamplexa*

17a. Grindelia inuloides var. **inuloides.**

Demetria spathulata Lag., Gen. Sp. Pl. (Lagasca), 30. 1816. TYPE: [Mexico.] Cultivated at Hort. Madrid., 1822, *J. D. Rodriguez s.n.* (neotype, designated here, MA [barcode] 240984 digital image!).

Grindelia angustifolia Kunth, Nov. Gen. Sp. [H. B. K.] 4: 244–245 (folio ed.). 1818. [also 4: 309–310 (quarto ed.). 1820.] *Grindelia arguta* Schrad. ex DC., Prodr. (DC.) 5: 315. 1836, nom. illeg. TYPE: Mexico. Michoacán: "prope Valladolid de Michoacán & Pazcuaro," s.d., *F. W. Humboldt & A. J. Bonpland s.n.* (holotype, B-W-16438-010 digital image!; isotypes, P [barcode] 00742791 digital image!, P [barcode] 00742794 digital image!).

Grindelia pubescens Nutt., J. Acad. Nat. Sci. Philadelphia 7: 74. 1834. TYPE: U.S.A. Arkansas: [Mexico, cf. Steyermark (1934: 454)], *T. Nuttall s.n.* (holotype, PH [barcode] 00047866!; isotype, GH [barcode] 00008437 digital image!).

Stems, leaves, and phyllaries with sessile glandular trichomes. Cauline leaves 0.5–5 × 0.2–2 cm, sometimes clasping. Chromosome number: $n = 6$ (Powell & Turner, 1963: 135; Semple et al., 1989: 302).

Iconography. Steyermark (1934: 457, fig. 1).

Distribution and habitat. *Grindelia inuloides* var. *inuloides* has been collected in the Federal District and in Guanajuato, Jalisco, Michoacán, Nuevo León, Queretaro, Sierra Madre Oriental, Puebla, and Veracruz (Mexico). The autonymic variety has been collected in pine and oak forests, from 1800 to 2350 m.

Phenology. *Grindelia inuloides* var. *inuloides* flowers from June to October.

Common names. Palancapatli de Puebla, gum daisy (<http://www.conabio.gob.mx/malezasdemexico/asteraceae/grindelia-inuloides/fichas/ficha.htm#1.Nombres>).

Discussion. Steyermark (1937: 226) stated that *Inula serrata* Pers. (nom. illeg., non *I. serrata* Gilib., Fl. Lit. Inch. I. 207. 1782) was based on *Grindelia inuloides*. However, Persoon (1807: 452) cited only "*Aster*, Lagasca. Hab. in N. Hispania," perhaps referring to a specimen sent to him by Lagasca from the Royal Botanical Garden of Madrid, sub nom. "*A. spathulata*," which may have corresponded to the plants upon which Lagasca described *Demetria spathulata*. No such specimen was located in the Persoon herbarium at L, so the identity of *I. serrata* remains uncertain.

Lagasca described *Demetria spathulata* based on a plant cultivated in the Royal Botanical Garden of Madrid from seed sent from Mexico by Martín Sessé in 1804, under the name "*Aster spathulatus*" (non *A. spathulatus* Lindl., 1834), whose offspring, cultivated at Berlin, constituted the type of *Grindelia inuloides*. No MA specimens appear to have been collected from the Royal Botanical Garden of Madrid between the years 1805 and 1816 with the name "*A. spathulatus*." If such specimens did exist, then the collection might have been in Lagasca's personal herbarium, which was destroyed in Seville during his escape from Spain in 1823. Nevertheless, a specimen with the name "*A. spatulatus*," which certainly does not belong to the same plant studied by Lagasca, but probably represents a descendant offspring, was collected from the Royal Botanical Garden of Madrid in 1822 by José Demetrio Rodriguez (when Lagasca was director

of the botanical garden). Thus we propose the *J. D. Rodriguez s.n.* specimen as neotype for *D. spathulata*.

With respect to the type of *Grindelia pubescens*, we agree with Steyermark (1934) in considering an error on the specimen label, which attributed its provenance from Arkansas (U.S.A.).

Additional specimens examined. MEXICO. **Distrito Federal:** along rte. 57, 29 mi. S of toll gate, N of Mexico City, *A. M. Powell & J. Edmondson 585* (TEX); 16 km NW of Toluca along rd. to Ixtlahuaca & 1 km E on side rd., *R. W. Sanders 1067* (TEX). **Guanajuato:** Mpio. Santa Ana, Rancho La Soledad, *C. L. Díaz Luna 13168* (TEX); Acámbaro, El Moral, *J. M. Escobedo 2509* (XAL); Las Palomas, *S. Gutierrez 1* (XAL); Puerto de Santa Rosa, *R. Gutiérrez s.n.* (XAL). **Jalisco:** 1 km adelante del Crucero a Arandas, carretera Tepatitlán–Pegueros, *R. Guzmán et al. 953* (XAL); Valle de Guadalupe, Campo Charro, carr. 80, entre Pegueros y Valle de Guadalupe, *A. Rodríguez et al. 1292* (XAL); near farmland, 42 mi. E of Guadalajara, *U. T. Waterfall 15641* (TEX). **Michoacán:** Distr. Zitacuaro, Zitacuaro–Jurungeo, *G. B. Hinton 11919* (TEX); Coeneo, Rancho Quenzio, *H. D. Barriga & N. López 2492* (XAL); Penjamillo, El Encinal, *E. Pérez & E. García 1632* (XAL). **Nuevo León:** Puerto Anteojos, Aramberri, *G. B. Hinton 20398* (TEX). **Puebla:** along rte. 150–140, 8 mi. E of Puebla, *A. M. Powell & J. Edmondson 616* (TEX). **Querétaro:** San Joaquín, 8 km al E de San Joaquín, sobre camino a Aguacate, *R. Fernández 4834* (XAL); Cadereyta, 500 m al W de Vizarrón, *S. Zamudio 2336* (XAL); Pinal de Amoles, *S. Zamudio 2663* (XAL). **Sierra Madre Oriental:** Cieneguillas to Puerto Santa Ana, 15 mi. SW of Galeana, *C. H. Mueller & M. T. Mueller 896* (TEX). **Veracruz:** Acultzingo, pass at Puebla–Veracruz border, ca. 4.4 mi. W of Acultzingo, *B. L. Turner 15329 with F. Barrie* (TEX, XAL); Acultzingo, La Barranca del Tule, 2350 m, *P. Ventura 15435* (XAL).

17b. Grindelia inuloides var. **glandulosa** (Greenm.) Steyerm., Ann. Missouri Bot. Gard. 21: 456. 1934. Basionym: *Grindelia glandulosa* Greenm., Proc. Amer. Acad. Arts 34: 575. 1899. TYPE: Mexico. Hidalgo: wet meadows, Sierra de Pachuca, 13 Aug. 1898, *C. G. Pringle 6962* (holotype, F [barcode] 0050295F digital image!, GH [barcode] 00008446!; isotypes, GOET [barcode] 001586 digital image!, JE [barcode] 00000621 digital image!, K [barcode] 000221372 digital image!, M [barcode] 0029680 digital image!, MEXU-30050 digital image!, MO-130326!, NY [barcode] 00169632 digital image!, P [barcode] 00742798 digital image!, PH [barcode] 00047856 digital image!, RSA [barcode] 0001222 digital image!, TEX [barcode] 00000477!, US [barcode] 00127637 digital image!). Figure 7.

Stems, leaves, and phyllaries with stipitate glandular trichomes. Cauline leaves 0.5–5 × 0.2–1.5 cm, clasping. Chromosome number not known.

Distribution and habitat. *Grindelia inuloides* var. *glandulosa* is known from Coahuila, Hidalgo, Nuevo León, Oaxaca, and Puebla (Mexico). The variety is found in open conifer forests of *Pinus*, *Abies* Mill., and *Picea*, from 2400 to 3100 m.

Phenology. *Grindelia inuloides* var. *glandulosa* has been collected in flower from the beginning of June to August.

Etymology. The epithet of the variety is taken from the Latin "glandulosum," meaning "gland bearing," and refers to the presence of the glandular trichomes on the stems, leaves, and phyllaries.

Additional specimens examined. MEXICO. **Coahuila:** Buenos Aires, mtns. E of Saltillo, *J. M. Kenoyer & W. E. Crum 2778* (GH). **Hidalgo:** Sierra de Pachuca, *C. G. Pringle 9913* (TEX). **Nuevo León:** Mpio. Galeana, ca. 5 mi. S of Tanquecillos on rd. betw. San Rafael jct. & Galeana, *G. L. Nesom et al. 7194* (TEX); Mpio. Zaragoza, N side of Peña Nevada at Puerto Pinos & jct. with rd. to Joya de San Diego, on rd. from San Antonio de Peña Nevada, *G. L. Nesom et al. 7105* (TEX). **Oaxaca:** fields along rte. 190, ca. 1 mi. N of Tamazulapan, *R. Merrill King 2934* (TEX); along rte. 190, 7 mi. E of Tierra Blanca, *A. M. Powell & J. Edmondson 714b* (TEX). **Puebla:** Boca del Monte, *C. A. Purpus 2466* (GH); Mpio. Caltepec, Rincón de la Hierba, la Mesa Chica at W de Caltepec, *P. Tenorio Lezama et al. 6733* (TEX).

17c. Grindelia inuloides var. **latamplexa** G. L. Nesom, Phytologia 68: 327. 1990. TYPE: Mexico. Querétaro: 2.7 km SW of Pinal de Amoles on Hwy. 120, 1.7 km NE of SARH forestry fire station, 27 Dec. 1980, *J. M. Canne-Hilliker & D. W. Woodland 1941* (holotype, F [barcode] 0050296F digital image!). Figure 8.

Stems, leaves, and phyllaries with stipitate glandular trichomes. Cauline leaves 3–6 × 2 cm, broadly clasping. Chromosome number not known.

Distribution and habitat. *Grindelia inuloides* var. *latamplexa* has been collected in pine and oak forests, from 2300 to 2400 m, in Querétaro (Mexico).

Phenology. *Grindelia inuloides* var. *latamplexa* was collected in flower in November and December, an unusual time of flowering for North American species of the genus.

Etymology. The name of the variety is taken from the Latin "latus," meaning "broad" or "wide," and "amplectens," meaning "clasping," which refers to the base of the leaves.

Additional specimens examined. MEXICO. **Querétaro:** 15 mi. W of Pinal de Amoles, *B. L. Turner 76-13* (TEX).

18. Grindelia laciniata Rydb., Fl. Rocky Mts., 848, 1066. 1917. TYPE: U.S.A. Utah: Montezuma

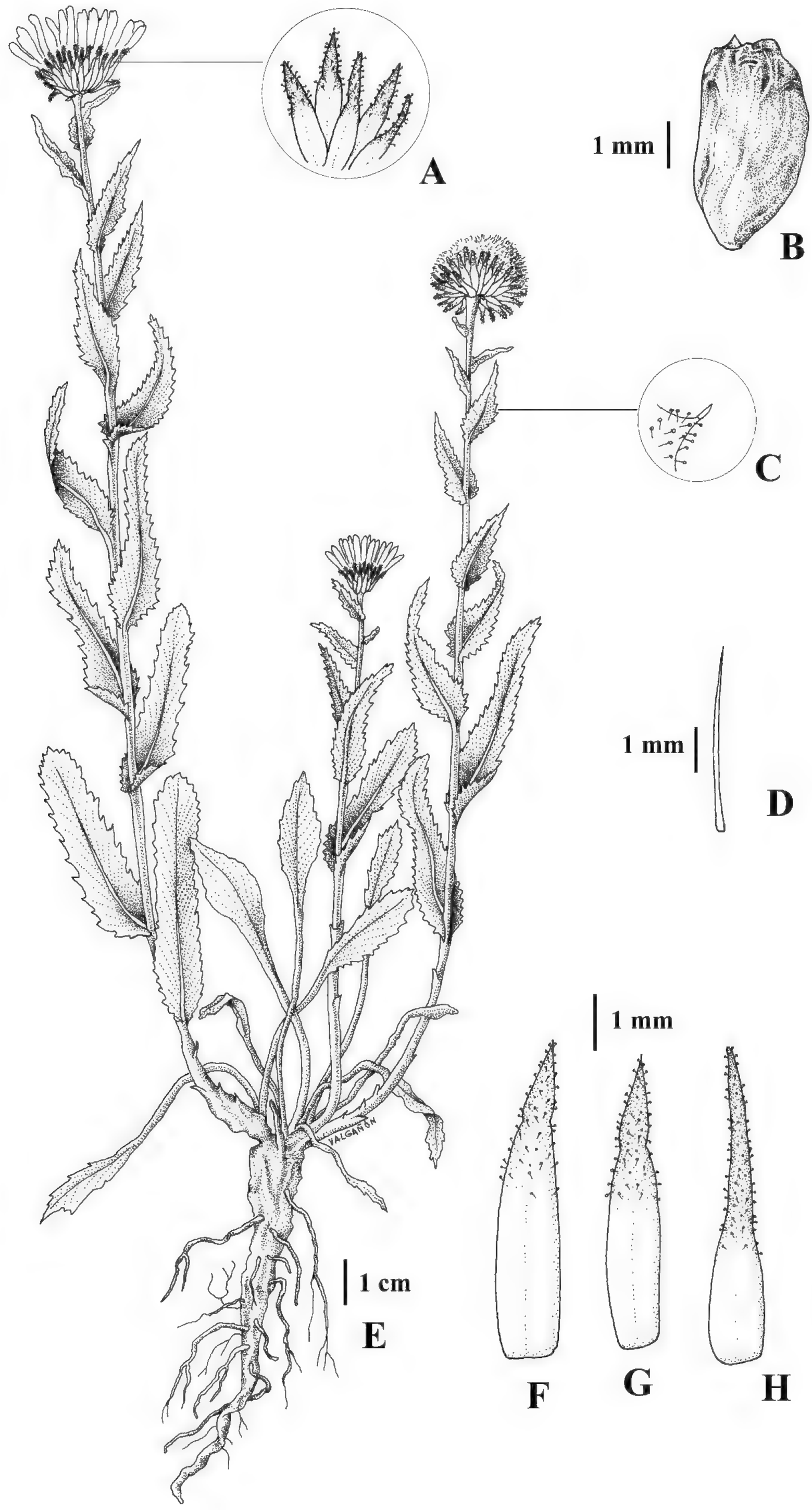

Figure 7. *Grindelia inuloides* Willd. var. *glandulosa* (Greenm.) Steyerm. —A. Part of the involucre, inner phyllary series represented. —B. Achene. —C. Leaf tooth, ending in a sclerotic tip, also covered with stipitate glandular trichomes. —D. Pappus, showing one of two smooth bristles. —E. Fertile habit. F–H. Representative phyllaries. —F. Inner series. —G. Middle series. —H. Outer series. Drawn from *R. Merrill King 2934* (TEX).

Canyon, E of Monticello, 2000 m, 13 Aug. 1911, *P. A. Rydberg 9692 with A. O. Garrett* (holotype, NY [barcode] 00169612 digital image!; isotypes, RM [barcode] 0001123 digital image!, US [barcode] 00127641 digital image!).

Perennial subshrubs, 0.25–0.3 m, with xylopodium; stems several, ramified, glabrous. Leaves herbaceous, sessile, linear to narrowly ovate; basal leaves pinnatisect, 2–4 × 0.2–1.5 cm: blade apex acute, margin toothed, teeth ending in a sclerotic tip, sessile glandular trichomes in pits on both blade surfaces. Heads radiate, pedunculate, 1 cm diam.; involucre hemispheric, scarcely resinous, 5–6 × 6–7 mm; phyllaries in 4 or 5 unequal series, graduated, subulate, subcoriaceous, linear-elliptic, 2.5–6 mm, spreading to reflexed, glabrous. Ray florets 12 to 15; tube glabrous, ligule elliptic, 7–10 mm, apex entire. Disk florets with corolla 4–5 mm, with a gradually ampliate throat. Achenes dark brown, elliptic, 4-angled, smooth, apex truncate; pappus of 2 setiform awns, 3–4 mm, barbellulate. Chromosome number: $2n = 12$ (Cronquist, 1994: 254).

Iconography. Steyermark (1934: 505, fig. 19); Cronquist (1994: 255).

Distribution and habitat. *Grindelia laciniata* grows on arid plains and canyons, at ca. 2000 m, in Utah (U.S.A.).

Phenology. *Grindelia laciniata* flowers from July to September.

Etymology. The specific epithet is taken from the Latin "laciniatus," meaning "slashed into narrow divisions with tapered, pointed incisions," which refers to the pinnatisect leaves.

Discussion. The differentiating characters of *Grindelia laciniata* include radiate heads with subulate phyllaries in a graduated series on the involucre, and leaves that are pinnatisect, with sessile glandular trichomes in pits. Strother and Wetter (2006) included this species in the synonymy of *G. arizonica*, but in this species the phyllaries are acuminate and the leaves are entire, with sessile glandular trichomes not in pits.

Additional specimens examined. U.S.A. **Utah:** San Juan Co., mesa E of Monticello, *P. A. Rydberg 9210* (NY); along US 163 N of Monticello, *M. A. Wetter 720* (NY); 2.9 mi. N of jct. with US 666 at Monticello, *M. A. Wetter 77* (NY), *M. A. Wetter 888* (NY).

19. Grindelia lanceolata Nutt., J. Acad. Nat. Sci. Philadelphia 7: 73. 1834. TYPE: U.S.A. [Arkansas or Oklahoma:] "Arkansas," s.d., *Dr. [Z.] Pitcher s.n.* (lectotype, designated here, PH [barcode] 01049678!; isolectotype, NY [barcode] 169613!).

Perennial subshrubs or shrubs; stems 1 to 5, ramified, glabrous or with scattered simple hairs. Leaves herbaceous or subcoriaceous, sessile, elliptic, narrowly oblong, oblong, broadly ovate, or triangular-ovate, clasping; blade apex acute, margin finely serrate, serrate, deeply toothed, or pinnatisect, rarely entire, teeth ending in a curved spinule, simple hairs absent or present along the main nerve, on the margins, or on both blade surfaces, sessile glandular trichomes, frequently in pits, on both surfaces. Heads radiate, pedunculate; involucre campanulate, resinous, 8–13 × 12–23 mm; phyllaries in 5 or 6 subequal series, acuminate, linear, 8–16 mm, glabrous, with sessile glandular trichomes in pits; apex spinulose; the outer bracts erect or reflexed, acumen linear, terete, 3–4 mm, about equal to the height of the disk; the inner bracts erect, exceeding the height of the disk. Ray florets 14 to 31; tube glabrous, ligule elliptic, 10–16 mm, apex entire. Disk florets with corolla 5–6 mm, with a gradually ampliate throat. Achenes elliptic, yellowish or brownish gray, somewhat flattened, 3- or 4-angled, striate, apices coronate or knobby; pappus of 2 setiform awns, 4–7 mm, smooth to barbellate.

Etymology. The specific epithet is taken from the Latin "lanceolatus," meaning "a shape broadest at the middle and tapering to each end," which refers to the lanceolate shape of the leaves.

Discussion. *Grindelia lanceolata* is characterized by its radiate heads, with acuminate phyllaries arranged in subequal series within the involucre. The phyllary acumen is linear; the leaves are entire or pinnatisect, with the marginal teeth ending in a curved spinule; the sessile glandular trichomes are frequently in pits on both blade surfaces; the achene has an either coronate or knobby apex.

Nuttall's protologue (1834: 73) for *Grindelia lanceolata* states "Hab. In Arkansas. T. Nuttall and Dr. Pitcher." We could not find a specimen of *G. lanceolata* collected by Nuttall in Arkansas, but there are two specimens of a Pitcher collection in NY and PH. We chose the PH specimen as lectotype because it has an original label with the name *G. lanceolata*, and it is representative of this species. The NY isolectotype also has on the same sheet a specimen (NY [barcode] 169614) collected by *T. Drummond* in Texas (n° 137).

Grindelia lanceolata is represented by four varieties that are geographically distinct. The autonymic variety has the broadest documented range, occurring in Alabama, Arkansas, Missouri, and

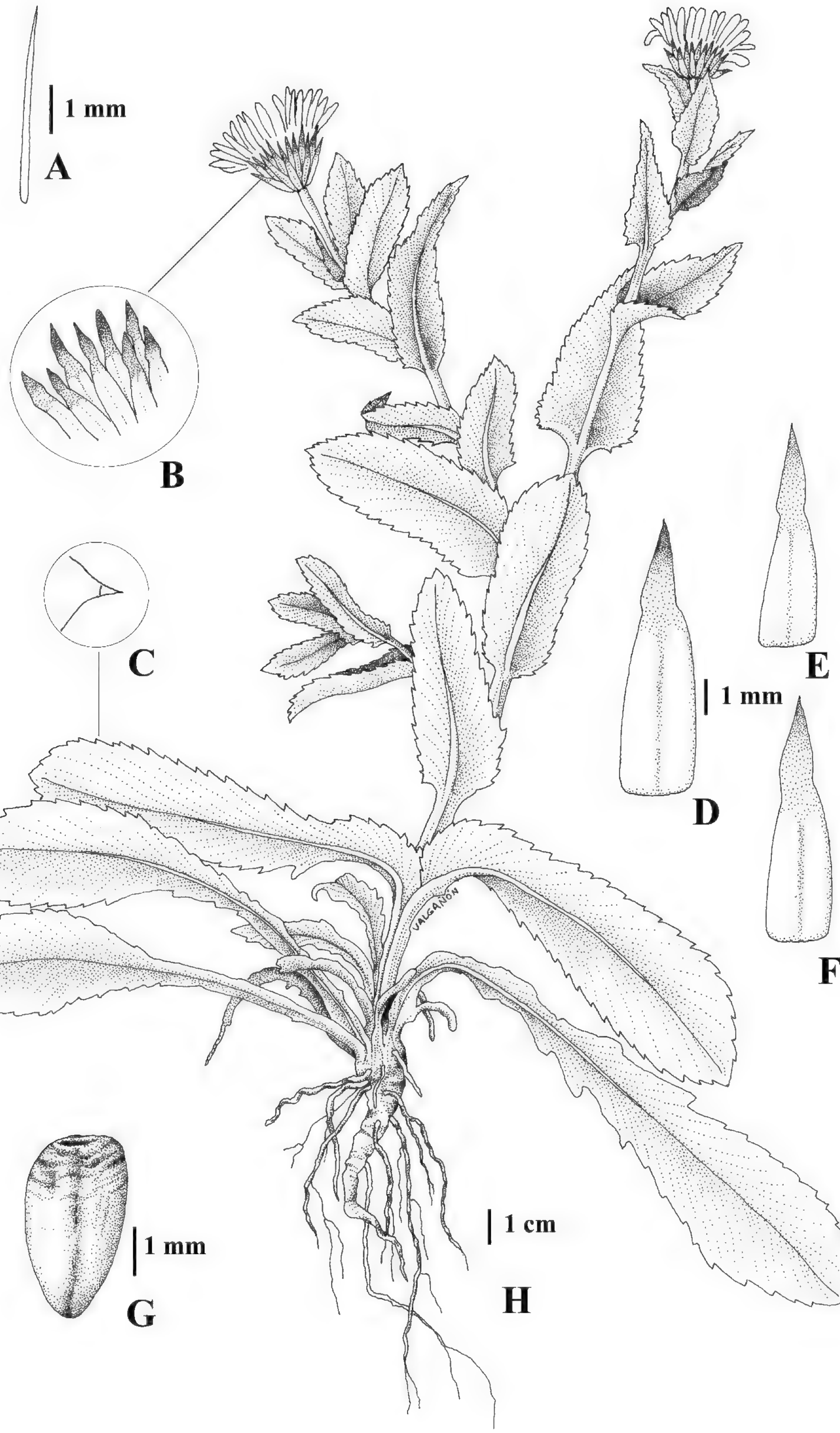

Figure 8. *Grindelia inuloides* Willd. var. *latamplexa* G. L. Nesom. —A. Pappus, showing one of two smooth bristles. —B. Part of the involucre, inner phyllary series represented. —C. Leaf tooth, ending in a sclerotic tip, also covered with stipitate glandular trichomes. D–F. Representative phyllaries. —D. Inner series. —E. Outer series. —F. Middle series. —G. Achene. —H. Fertile habit. Drawn from *B. L. Turner 76-13* (TEX).

Oklahoma. *Grindelia lanceolata* var. *greenei* (Steyerm.) G. L. Nesom has the southernmost distribution, collected from Nuevo León, Mexico; *G. lanceolata* var. *subincisa* is known from Colorado and New Mexico. *Grindelia lanceolata* var. *texana* naturally occurs in Texas and Oklahoma, extending south to Coahuila, Mexico. Four varieties are recognized within *G. lanceolata* and are distinguished by the following key couplets.

1a. Basal leaves deeply toothed to pinnatisect; heads less than 2.5 cm diam .... 19c. *G. lanceolata* var. *subincisa*
1b. Basal leaves toothed, serrate, or minutely serrate; heads 2.5–3.5 cm diam.
  2a. Leaves triangular-oblong, margins irregularly toothed ..... 19d. *G. lanceolata* var. *texana*
  2b. Leaves narrowly oblong to ovate-elliptic, margins serrate.
    3a. Basal and middle leaves narrowly oblong, oblong, or ovate-elliptic, 3.5–11 cm, margins serrate; heads 2.5–3.5 cm diam ..... 19a. *G. lanceolata* var. *lanceolata*
    3b. Basal and middle leaves broadly ovate-elliptic, 1.9–2.9 cm, margins minutely serrate; heads 2.5–2.7 cm diam .... 19b. *G. lanceolata* var. *greenei*

19a. Grindelia lanceolata var. **lanceolata.**

Grindelia littoralis Steyerm., Ann. Missouri Bot. Gard. 21: 516. 1934. TYPE: U.S.A. Texas: Galveston Bay, 20 Sep. 1884, *J. F. Joor s.n.* (holotype, MO-130019!; isotype, MO-130018 digital image!).

Grindelia lanceolata Nutt. f. *latifolia* Steyerm., Ann. Missouri Bot. Gard. 21: 515. 1934, syn. nov. TYPE: U.S.A. Missouri: Stone Co., Marble Cave, 11 Sep. 1898, *W. Trelease s.n.* (holotype, MO [barcode] 714089!).

Shrubs 0.3–1.5 m. Leaves narrowly oblong, oblong, or ovate-elliptic, 3.5–11 × 0.35–2 cm, margin serrate. Heads 2.5–3.5 cm diam. Chromosome numbers: $n = 6$ (Dunford, 1986: 303); $2n = 12$ (Whitaker & Steyermark, 1935: 71; Dunford, 1969: 20).

Iconography. Steyermark (1934: 518, fig. 22; 1972: 1479, pl. 351, fig. 5).

Distribution and habitat. *Grindelia lanceolata* var. *lanceolata* grows on rocky slopes, prairies, nude and degraded soils, from 0 to 700 m, in Alabama, Arkansas, Missouri, and Oklahoma (U.S.A).

Phenology. *Grindelia lanceolata* var. *lanceolata* has been collected in flower from the beginning of July to October.

Common names. Narrow-leaf gumweed (<http://plants.usda.gov/>), spiny-tooth gumweed (<http://www.unl.edu/agnicpls/gpcn/lating/>; <http://wisplants.uwsp.edu>).

Additional specimens examined. U.S.A. **Alabama:** Franklin Co., *R. Kral 44003* (MO). **Arkansas:** Independence Co., beside Green Creek, on way to Batesville, *R. D. Thomas 20565* (MO); Independence, Polk Bayou, E of Cushman, spoil bank area at old manganese mine, *R. D. Thomas & R. Reid 20964* (XAL). **Missouri:** Barry Co., 21 Aug. 1892, *F. M. Diwart s.n.* (MO-129990); dolomite ledges & slopes, bald knobs near Seligman, *E. J. Palmer 29364* (MO); rocky slopes, bald knobs, near Eagle Rock, *E. J. Palmer 31465* (MO); Johnson Co., field bordering upland prairie thickets, 2 mi. W of Warrensburg, *J. A. Steyermark 24602* (MO); McDonald Co., shale outcrops, hillsides, Noel, *E. J. Palmer 4161* (MO); Ozark Co., rocky open ground, bald knobs, bald Jesse near Gainesville, *E. J. Palmer 33055* (MO); St. Louis Co., *M. C. Lodewyks 80* (MO); Taney Co., Hughie Bald, near Branson, *M. A. Wetter 483* (MO); 1/2 mi. E of Table Rock Dam, *P. L. Redfearn Jr. 33149* (MO). **Oklahoma:** Creek Co., Sapulpa, *B. F. Bush 220* (MO).

19b. Grindelia lanceolata var. **greenei** (Steyerm.) G. L. Nesom, Phytologia 68: 324. 1990. Basionym: *Grindelia greenei* Steyerm., Ann. Missouri Bot. Gard. 21: 517. 1934. TYPE: Mexico. Nuevo León: vic. Monterrey, 1924, *C. R. Orcutt 1204* (holotype, US [barcode] 00127638 digital image!).

Shrubs 1.2 m. Leaves broadly ovate-elliptic, 1.9–2.9 × 1–1.5 cm, margins with small regular teeth. Heads 2.5–2.7 mm diam. Chromosome number not known.

Iconography. Steyermark (1934: 518, fig. 23).

Distribution and habitat. *Grindelia lanceolata* var. *greenei* has been collected in Nuevo León (Mexico).

Phenology. *Grindelia lanceolata* var. *greenei* flowers at the beginning of October.

Etymology. *Grindelia lanceolata* var. *greenei* was named in honor of Edward Lee Greene (1843–1915), first professor of botany at the University of California, Berkeley. He collected in the western United States, from states such as Colorado, New Mexico, and California.

Additional specimen examined. MEXICO. **Nuevo León:** Mpio. Monterrey, 9 Oct. 1937, *L. A. Kenoyer s.n.* (MO-1136023).

19c. Grindelia lanceolata var. **subincisa** (Greene) Adr. Bartoli & Tortosa, comb. nov. Basionym: *Grindelia subincisa* Greene, Pittonia 4: 154–155. 1900. *Grindelia decumbens* Greene var. *subincisa* (Greene) Steyerm., Ann. Missouri Bot. Gard. 21: 503–504. 1934. TYPE: U.S.A. New Mexico: Chama, 5 Sep. 1899, *C. F. Baker 683*

(lectotype, designated here, NDG-47371 digital image!; isolectotypes, F [barcode] 0050293F digital image!, GH [barcode] 00008442!, MO-130298!, NDG-53651 digital image!, NDG-53652 digital image!, NY [barcode] 169630!, RM [barcode] 0001131 digital image!, RSA [barcode] 0001220 digital image!, US [barcode] 00127660 digital image!, US [barcode] 00369208 digital image!). Figure 9.

Subshrubs 0.24–0.40 m. Leaves elliptic, 2–6 × 0.3–0.75 cm, margins deeply toothed to pinnatisect. Heads less than 2.5 cm diam. Chromosome number not known.

Distribution and habitat. *Grindelia lanceolata* var. *subincisa* has been collected along streams and lowlands, from 2000 to 2300 m, in Colorado and New Mexico (U.S.A.).

Phenology. *Grindelia lanceolata* var. *subincisa* has been collected in flower from July to September.

Etymology. The name of this variety is taken from the Latin "incisus," meaning "cut deeply and sharply," which refers to the degree of division of the leaf blade.

Discussion. For *Grindelia subincisa*, Greene's protologue does not state a collection, but Wooton and Standley (1915: 655) indicated the collection *C. F. Baker 683* as the type, and this opinion is followed here. In the Greene Herbarium at NDG, there are three specimens of *G. subincisa* collected by Baker on 5 September 1899 at Chama, probably all representing the same collection, and all three sheets correspond to the protologue. We chose the NDG sheet with barcode number 47371 as lectotype, because it is the only sheet that includes the collector number 683 on the label.

This taxonomic entity was later considered a variety of *Grindelia decumbens* by Steyermark (1934), but the species differs from *G. lanceolata* by its phyllaries with a triangular, subterete acumen, and the phyllaries arranged in a graduated series in the involucre. The leaves in *G. decumbens* have marginal teeth that end in a sclerotic tip. In *G. lanceolata*, the phyllaries have a spinulose tip arranged in five or six subequal series.

Additional specimens examined. U.S.A. **Colorado:** Conejos Co., 13.3 mi. NE of Conejos–Archuleta Co. line, *M. A. Wetter 956* (NY); La Plata Co., 9.6 mi. E of La Plata–Montezuma Co. line, *M. A. Wetter 964* (NY); Mineral Co., 28.3 mi. NW of Mineral–Río Grande Co. line, *M. A. Wetter 961* (NY). **New Mexico:** Río Arriba Co., along cumbers, Toltec Scenic Railway at Sublette NM Station, *M. A. Wetter 1031* (NY).

19d. Grindelia lanceolata var. **texana** (Scheele) Shinners, Field & Lab. 19: 78. 1951. *Grindelia texana* Scheele, Linnaea 21: 601. 1848. TYPE: U.S.A. Texas: 1846, *F. Lindheimer 418* (lectotype, designated here, US [barcode] 00127662 digital image!; isolectotypes, G [barcode] 00301851 digital image!, GH [barcode] 00283064 [p.p. with C. Wright, 1845] digital image!, GH [barcode] 00283066 not seen, GH [barcode] 00283067 not seen, PH [barcode] 01049683 digital image!).

Shrubs 0.45–0.9 m. Leaves triangular-oblong, 2–5 × 0.7–1.5 cm, margins irregularly toothed. Heads 2.5–3.5 cm diam. Chromosome numbers: $n = 6$ (Dunford, 1986: 20, sub *Grindelia texana*); $2n = 12$ (Dunford, 1969: 20, sub *G. texana*).

Iconography. Steyermark (1934: 518, fig. 21), sub nom. *Grindelia texana.*

Distribution and habitat. *Grindelia lanceolata* var. *texana* has been collected from prairies, valleys with *Juglans* L., and low hills, from 850 to 1000 m, in Oklahoma and Texas (U.S.A.) and Coahuila (Mexico).

Phenology. *Grindelia lanceolata* var. *texana* has been collected in flower from the beginning of June to September.

Etymology. The specific epithet refers to the state of Texas in the United States, from which the type specimen was collected.

Discussion. The holotype of *Grindelia texana* was not found at TEX, and the Scheele Herbarium has apparently been destroyed, or is at least missing at TEX (Tom Wendt, curator, personal communication). There are specimens of this species collected by F. Lindheimer in Texas during 1846 at G, GH, PH, and US, which predate the protologue. We chose as lectotype the US specimen as representative of this taxon.

We recognize *Grindelia texana* as a variety of *G. lanceolata* because they share similar heads, leaves with sessile glandular trichomes in pits, and differ from the typical variety only by the triangular-oblong shape of the leaves, which are irregularly toothed in the margin.

Additional specimens examined. MEXICO. **Coahuila:** W slopes of Sierra del Carmen, 8 km E of Hacienda Encantada, *R. M. Stewart 1702* (GH); 21 km S by winding rd. from Rancho Chupadero del Caballo toward Las Norias, *F. Chiang, T. Wendt & M. C. Johnston 9170* (NY). U.S.A. **Oklahoma:** Garvin Co., limestone hills, Arbuckle Mtns. near Turner Falls State Park, *E. J. Palmer 42014* (MO); Murray Co., Arbuckle Mtns., *D. Demare 13192* (PH); at Turner Falls Park scenic overlook, *M. A. Wetter 1008* (NY). **Texas:** Blanco Co., Blanco, dry hillsides, *E. J. Palmer*

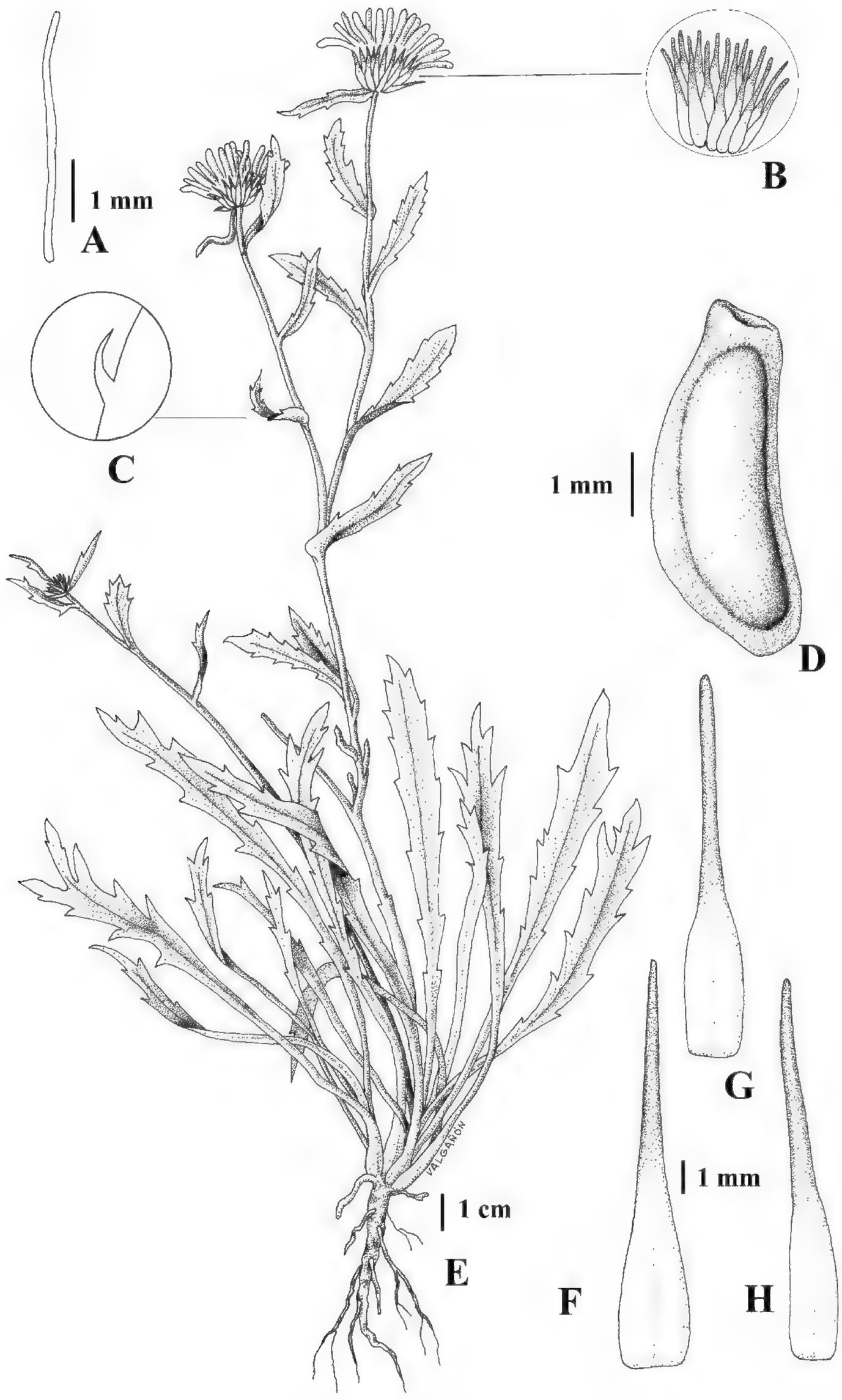

Figure 9. *Grindelia lanceolata* Nutt. var. *subincisa* (Greene) Adr. Bartoli & Tortosa. —A. Pappus, showing one of two setiform awns. —B. Involucre, with phyllaries in five or six series. —C. Leaf tooth, ending in a curved spinule. —D. Achene, somewhat flattened, 3- or 4-angled. —E. Fertile habit. F–H. Representative phyllaries. —F. Outer series. —G. Middle series. —H. Inner series. Drawn from *M. A. Wetter 1031* (NY).

12855 (MO); Burnet Co., Burnet, dry calcareous open ground, *E. J. Palmer 10249* (MO); Collin Co., Coit Meadow on Renner Rd., *C. L. Lundell 18644* (PH); Dallas Co., Dallas, *M. R. Stephenson 126* (MO); Erath Co., 1.3 mi. S of Erath–Palo Pinto Co. line, *M. A. Wetter 1010* (NY); Hopkins Co., 1 mi. E of Mount Vernon, 25 June 1949, *C. I. Stittler s.n.* (PH-837382); Kendall Co., Boerne, *F. W. Pennell 5478* (NY).

20. Grindelia leptocarpa (De Jong & Beaman) Adr. Bartoli & Tortosa, comb. nov. Basionym: *Olivaea leptocarpa* De Jong & Beaman, Brittonia 15: 91–92. 1963. TYPE: Mexico. Durango: in wet valley, in pond along hwy. 45, 43.4 mi. N of Ciudad Durango, 7 Aug. 1961, *D. C. D. De Jong & E. K. Longpre 971* (holotype, MSC [barcode] 0092488 digital image!; isotypes, GH [barcode] 00010747!, US [barcode] 00124576!).

Aquatic rhizomatous herbs, 0.8 m; stems 1 or 2, scarcely ramified, glabrous, fistulose. Leaves herba-

ceous, sessile, linear to linear-oblong or fiddle-shaped, clasping; blade apex obtuse, with stipitate glandular trichomes when young, margin entire or serrate, teeth ending in a sclerotic tip; basal leaves 2.8–4.1 × 0.25–0.5 cm; cauline leaves 0.8–2.3 × 0.1–0.25 cm. Heads radiate, pedunculate, 2–3 cm diam.; involucre hemispheric, scarcely resinous, 4–7 × 10–15 mm; phyllaries in 3 or 4 subequal series, chartaceous, triangular to narrowly triangular, 3–5 mm, subulate, erect, apex herbaceous, with stipitate glandular trichomes. Ray florets 35 to 50; tube with stipitate glandular trichomes, ligule linear-elliptic, 6.5–9.5 mm, apex 3-toothed. Disk florets with corolla 3–3.8 mm, with a gradually ampliate throat, tube with stipitate glandular trichomes. Achenes elliptic, brownish green, 2-angled, flattened, 3–3.6 mm, smooth, apex truncate; pappus of 2 to 5 bristles, 3–3.8 mm, barbellulate. Chromosome number: $n = 6$ (De Jong & Beaman, 1963: 91, sub nom. *Olivaea leptocarpa*).

Iconography. De Jong and Beaman (1963: 89, figs. 10–18).

Distribution and habitat. *Grindelia leptocarpa* has been collected from alkaline lowlands, at ca. 1780 m, in Durango (Mexico).

Phenology. *Grindelia leptocarpa* flowers from August to October.

Etymology. The specific epithet is taken from the Latin "lepto-," meaning "slender, thin, or narrow," and from "-carpus," meaning "fruit," which refers to the flattened achenes.

Discussion. *Grindelia leptocarpa* and *G. tricuspis* are distinct from other species of the genus in their aquatic habit and fistulose stems. For this reason they were both described under the genus *Olivaea*, as a genus distinct from *Grindelia*. Different authors do not agree with the recognition of both genera (McVaugh, 1984; Nesom, 1997), but others have considered them as different (De Jong & Beaman, 1963; Lane & Hartman, 1996; Nesom, 2000; Nesom & Robinson, 2007). We consider it cautious to include this species in the genus *Grindelia* until more evidence is available, since the characters of the heads (radiate, with acuminate or subulate phyllaries), the pappus (composed of caducous bristles), and the achenes (glabrous, not costate) fit those of the genus *Grindelia*.

Additional specimen examined. MEXICO. **Durango:** along Hwy. 45 N of Durango, *R. D. Worthington 8963* (NY).

21. Grindelia macvaughii G. L. Nesom, Phytologia 68: 312. 1990. TYPE: Mexico. Jalisco: 15.9 km E of Agua El Obispo (W of Lagos de Moreno) on Hwy. 80, ditch on NW side of rd., 1770 m, 20 Aug. 1979, *M. A. Lane 2594* (holotype, TEX [barcode] 00373593!). Figure 10.

Annual or biannual subshrubs, 0.3–0.9 m; stems several, prostrate with tips rising upward, ramified, glabrous, with sessile glandular trichomes. Leaves sessile, subcoriaceous, narrowly oblong, oblong-elliptic, or narrowly elliptic, 2–3.5 × 0.4–0.7 cm, clasping; blade apex acute or obtuse, margin scabrous, finely serrate, teeth ending in a sclerotic tip, sometimes spinescent, sessile glandular trichomes scattered on both blade surfaces. Heads radiate, subsessile, 1.2–1.7 cm diam.; involucre hemispheric-campanulate, resinous, 5–7 × 9–10 mm; phyllaries in 3 or 4 unequal series, abruptly graduated, acuminate, narrowly ovate; acumen flat to subterete, 1–3 mm, with sessile glandular trichomes in pits; the outer bracts 2–5 mm, spreading or reflexed; the upper phyllaries 7–9 mm, erect. Ray florets 15 to 25; tube glabrous, ligule narrowly elliptic, 12–18 mm, apex entire. Disk florets with corolla 5–6 mm, with a gradually ampliate throat. Achenes brown, subquadrate, 2.5–3.5 mm, with prominent transverse incisions and broad, shallow longitudinal furrows; pappus of 2 setiform awns, 5–6 mm, straight, smooth. Chromosome number not known.

Distribution and habitat. *Grindelia macvaughii* has been collected in the surroundings of Lagos de Moreno and found on desert lands, prairies, and pastures, from 1800 to 1900 m, in Jalisco (Mexico).

Phenology. *Grindelia macvaughii* has been collected in flower from August to October.

Etymology. *Grindelia macvaughii* was named in honor of Rogers McVaugh (1909–2009), research professor of botany at the UNC Herbarium, curator of Mexican plants, and professor emeritus of botany at the University of Michigan.

Discussion. Useful characters for distinguishing *Grindelia macvaughii* are its radiate, subsessile heads and hemispheric-campanulate involucre. The phyllaries are arranged in abruptly graduate series in the involucre, the phyllary acumen is flat or subterete, and the outer phyllaries are spreading or reflexed. The marginal teeth of leaves end in a sclerotic tip and are sometimes spinescent.

Grindelia macvaughii is close to *G. oxylepis*, sharing an annual or biannual habit, radiate heads with the phyllaries of the involucre arranged in abruptly graduated series, and pappus of two or three setiform awns. *Grindelia macvaughii* differs by the

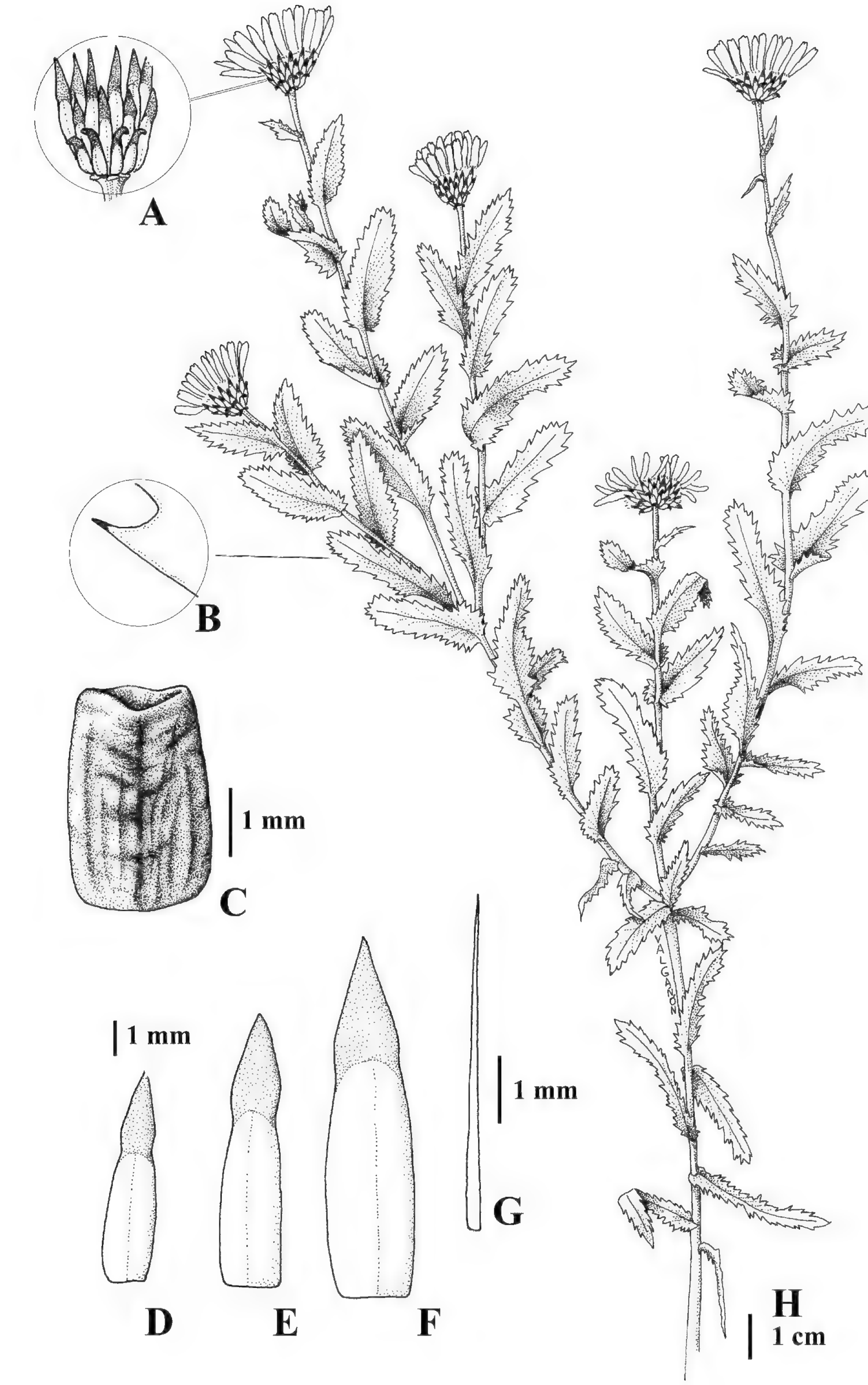

Figure 10. *Grindelia macvaughii* G. L. Nesom. —A. Involucre, with phyllaries in three or four series. —B. Leaf tooth ending in a sclerotic tip, sometimes spinescent. —C. Achene, subquadrate, with prominent transverse incisions and longitudinal furrows. D–F. Representative phyllaries. —D. Outer series. —E. Middle series. —F. Inner series. —G. Pappus, showing one of two setiform awns. —H. Fertile habit. Drawn from *R. McVaugh 12820* (TEX).

nonpunctate leaves with marginal teeth that end in a sclerotic tip (vs. punctate leaves with marginal teeth that end in a group of sessile glandular trichomes) and the acuminate (vs. subulate) phyllaries.

Additional specimens examined. MEXICO. **Jalisco:** ca. 11 mi. SE of Lagos de Moreno, near hwy. to León, *R. McVaugh 12820* (TEX); grassland with desert shrubs, 11 mi. SE of Lagos de Moreno, *U. T. Waterfall 13869 with C. S. Wallis* (TEX).

22. Grindelia microcephala DC., Prodr. (DC.) 5: 315. 1836. *Grindelia inuloides* Willd. var. *microcephala* (DC.) A. Gray in Torr., Rep. U.S. Mex. Bound., Bot. [Emory] 2(1): 81. [July–Dec.] 1858. [1859]. TYPE: U.S.A. Texas: 1832, *J. L. Berlandier 2057* (holotype, G-DC, IDC microfiche!; isotypes, GH [barcode] 00008431!, NY [barcode] 00169615!, P [barcode] 00742802 ["in campis, July 1829"?] digital image!). Figure 11.

Annual subshrubs, 0.25–0.4 m; stem 1, erect, ramified, with simple hairs, villous or lanuginous. Leaves subcoriaceous, sessile, oblong or spatulate, 1–3 × 0.7–2 cm, clasping; blade apex acute to obtuse, margin denticulate-crenate, teeth ending in a group of sessile glandular trichomes, simple hairs and sessile glandular trichomes in pits on both surfaces. Heads radiate, shortly pedunculate, 0.8–1.2 cm diam.; involucre hemispheric, scarcely resinous, 6–9 × 8–13 mm; phyllaries in 5 or 6 subequal series, subulate, narrowly ovate, 6–9 mm, erect or spreading, glabrous, apex flat to subterete, erect or somewhat curved, with sessile glandular trichomes. Ray florets 16 to 27; tube glabrous, ligule elliptic, 6–10 mm, apex entire. Disk florets with corolla 4–5 mm, with a gradually ampliate throat. Achenes brown, globose, 3- or 4-angled, smooth or slightly rugose, apex truncate or with a small crown; pappus of 2 or 3 setiform awns, 4–6 mm, straight or weakly contorted, smooth. Chromosome number: $2n = 12$ (Dunford, 1969: 20).

Distribution and habitat. *Grindelia microcephala* grows on rich and humid soils, from 0 to 500 m, in Texas (U.S.A.).

Phenology. *Grindelia microcephala* flowers from June to August.

Etymology. The specific epithet is taken from the Latin "micro-," meaning "little, small," and "-cephalus" or "headed," which refers to the size of the heads.

Common name. Little head gumweed (<http://www.nic.funet.fi/pub/sci/bio/life/plants>).

Discussion. *Grindelia microcephala* is related to *G. adenodonta* and *G. pusilla*. The three species are annual subshrubs with radiate heads smaller than 1.5 cm diameter, with subulate phyllaries arranged in subequal series within the involucre. *Grindelia microcephala* and *G. pusilla* have achenes with two or three setiform awns, in contrast to the achenes of *G. adenodonta*, which are topped by two subulate scales. The achenes are slightly rugose in *G. microcephala* and sharply cut with transverse furrows in *G. pusilla*.

Additional specimens examined. U.S.A. **Texas:** Pleasanton Rd., 6 mi. S of San Antonio, 8 Aug. 1931, *M. C. Metz s.n.* (NY); Comal Co., New Braunfels, 7 Aug. 1938, *E. Ammerman s.n.* (MO-1102038); Dimmit Co., Carrizo Springs, 26 Apr. 193?, *E. Marcus & A. M. Jones s.n.* (MO-1012870); Uvalde Co., 1/2 mi. W of Uvalde, *J. A. Moore & J. A. Steyermark 3004* (MO).

23. Grindelia nana Nutt., Trans. Amer. Philos. Soc. 7: 314. 1841. TYPE: U.S.A. Oregon: Vancouver, *T. Nuttall s.n.* (lectotype, designated here, BM [barcode] 001025302 digital image!; isolectotype, GH [barcode] 00037702!).

Perennial subshrubs, 0.25–0.4(–0.8) m; stems several, somewhat decumbent at the base, single or ramified, glabrous. Leaves herbaceous, sessile; blade apex acute, mucronate, margin entire or toothed, teeth ending in a sclerotic tip, with sessile glandular trichomes in pits on both surfaces, sometimes with simple hairs on the margin; basal leaves narrowly obovate to narrowly elliptic, 3–9 × 0.4–1 cm, attenuate into a pseudopetiole; cauline leaves linear to narrowly elliptic, 0.7–4 × 0.3–0.5 cm. Heads radiate or discoid, pedunculate; involucre hemispheric-campanulate, resinous, 7–10 × 7–10 mm; phyllaries in 5 to 7 unequal series, graduated, acuminate, narrowly ovate, 3.5–10 mm, reflexed, glabrous; acumen terete, 1–1.5 mm, abruptly revolute, with sessile glandular trichomes. Ray florets present or absent. Disk florets with corolla 4–5 mm, with an abruptly ampliate throat. Achenes narrowly elliptic, dull brown, 4-angled, 3–4 mm, smooth, with knobs or a crown at the apex; pappus of 2 setiform awns, 3–5.5 mm, curved, smooth to barbellulate.

Etymology. The specific epithet refers to the small size of the plants and is derived from the Latin "nanus," meaning "dwarf."

Discussion. *Grindelia nana* is recognized by its small heads with the acuminate and reflexed phyllaries in five to seven graduated series, with the abruptly revolute acumen. Its leaves have sessile glandular trichomes in pits on both surfaces, and the blade margin presents teeth that end in a sclerotic

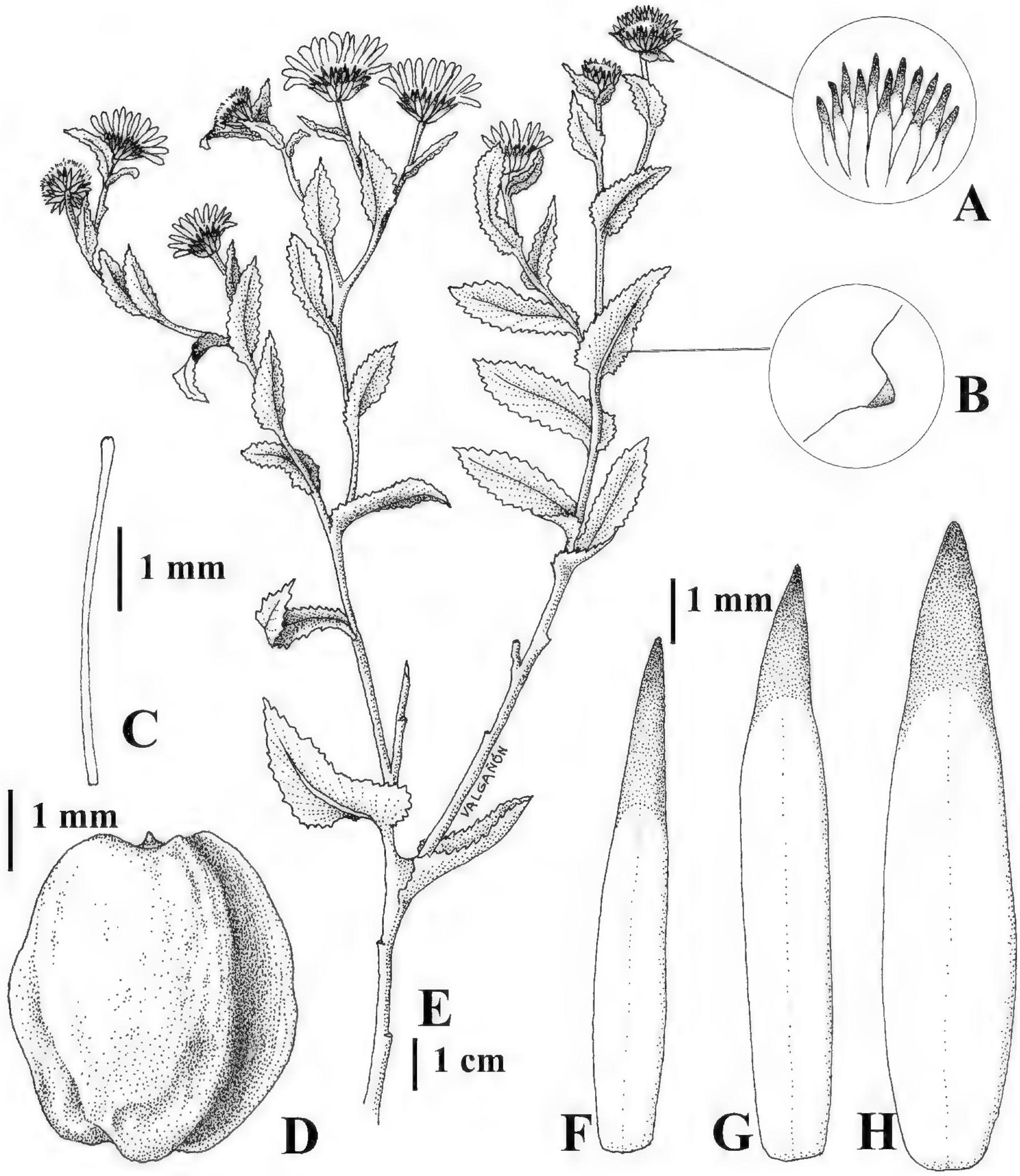

Figure 11. *Grindelia microcephala* DC. —A. Part of the involucre, inner phyllary series represented. —B. Leaf tooth, ending in a group of sessile glandular trichomes. —C. Pappus, showing one of two or three setiform awns. —D. Achene, showing the smooth or slightly rugose surface, 3- or 4-angled. —E. Fertile habit. F–H. Representative phyllaries. —F. Outer series. —G. Middle series. —H. Inner series. Drawn from *J. A. Moore & J. A. Steyermark 3004* (MO).

tip. The taxon is related to *G. fastigiata*, sharing the arrangement and form of the phyllaries, the presence of pits in the leaves, and the ending of marginal teeth of the blades. *Grindelia nana* differs by the pedunculate smaller heads only 7–10 mm (vs. the larger sessile or subsessile heads in *G. fastigiata*, 10–14 × 9–17 mm). Achenes are 4-angled in *G. nana*, but are 2-angled in *G. fastigiata*.

Strother and Wetter (2006) included *Grindelia nana* in the synonymy of *G. hirsutula*, but both species are quite distinct. In *G. hirsutula*, the phyllaries are subulate (vs. acuminate in *G. nana*), the corolla of disk florets has a gradually ampliate throat (vs. abruptly ampliate in *G. nana*), and the pappus is comprised of two to four subulate scales (vs. two setiform awns in *G. nana*).

We identified two candidate type collections by Nuttall from Vancouver. One sheet (*Nuttall s.n.*) was found at BM and matches the protologue of *Grindelia nana* (with leaves serrate). The *Nuttall s.n.* collection seen at GH was more variable, with three stems with the leaves entire and one stem with serrate leaves. We designated a lectotype for *G. nana* from the more representative specimen at BM. The sheet at GH (00037702) with the serrate-leaved stem is regarded as a duplicate and isolectotype for *G. nana* var. *nana*.

The Nuttall specimen at GH (*Nuttall s.n.*, GH-00037703) with stems bearing leaves with entire margins is designated as the lectotype of *G. nana* var. *integrifolia* Nutt.

Two varieties are recognized for *Grindelia nana*, as distinguished by the following couplet:

1a. Heads radiate ..... 23a. *G. nana* var. *nana*
1b. Heads discoid ..... 23b. *G. nana* var. *columbiana*

23a. Grindelia nana var. **nana.**

Grindelia nana Nutt. var. *integrifolia* Nutt., Trans. Amer. Philos. Soc. 7: 314. 1840. *Grindelia squarrosa* (Pursh) Dunal var. *integrifolia* (Nutt.) B. Boivin, Phytologia 23(1): 14. 1972. TYPE: U.S.A. Oregon: Vancouver, *T. Nuttall s.n.* (lectotype, designated here, GH [barcode] 00037703!).

Grindelia brownii A. Heller, Bull. Torrey Bot. Club 26: 315. 1899, syn. nov. *Grindelia nana* Nutt. f. *brownii* Steyerm., Ann. Missouri Bot. Gard. 21: 542. 1934. TYPE: U.S.A. Idaho: Nez Perces Co., 3500 ft., 14 July 1896, *A. A. Heller & E. G. Heller 3418* (holotype, NY [barcode] 00169598!; isotypes, MO [barcode] 714455 digital image!, NY [barcode] 169599!, UC [barcode] 87893 digital image!, US [barcode] 00432664 digital image!).

Grindelia integerrima Rydb., Bull. Torrey Bot. Club 37: 128. 1910, syn. nov. *Grindelia nana* Nutt. var. *integerrima* (Rydb.) Steyerm., Ann. Missouri Bot. Gard. 21: 546. 1934. TYPE: U.S.A. Idaho: Kootenai Co., sandy soil near Granite Station, 29 July 1892, *J. H. Sandberg, D. T. McDougal & A. A. Heller 784* (holotype, NY [barcode] 00169605!; isotypes, BM [barcode] 001025304 digital image!, CAS [barcode] 00123712 digital image!, F [barcode] 0050287F digital image!, MO [barcode] 714086 digital image!, NY [barcode] 169605!, PH [barcode] 47859!, US [barcode] 00008209 digital image!).

Grindelia nana Nutt. var. *altissima* Steyerm., Ann. Missouri Bot. Gard. 21: 544. 1934, syn. nov. TYPE: U.S.A. California: Humboldt Co., Eel River, at mouth of Laribee Creek, 200 ft., 12 Sep. 1915, *J. P. Tracy 4669* (holotype, UC [barcode] 186459 digital image!; isotypes, US [barcode] 01200337 digital image!, WTU [barcode] 206930 digital image!).

Grindelia nana Nutt. f. *puberula* Steyerm., Ann. Missouri Bot. Gard. 21: 545. 1934, syn. nov. [described under *Grindelia nana* var. *altissima*]. TYPE: U.S.A. California: Lake Co., Kenseyville, 12 June 1924, *J. W. Blankinship s.n.* (holotype, CAS [barcode] 00123667 digital image!).

Grindelia nana Nutt. f. *longisquama* Steyerm., Ann. Missouri Bot. Gard. 21: 543. 1934, syn. nov. TYPE: U.S.A. Idaho: Nez Perce Co., Clearwater, s.d., *R. Spalding s.n.* (holotype, GH [barcode] 00037704!, isotypes, GH [barcode] 00037713 digital image!, GH [barcode] 00037714 digital image!, NY [barcode] 00169618!).

Grindelia nana Nutt. var. *turbinella* Steyerm., Ann. Missouri Bot. Gard. 21: 545. 1934, syn. nov. TYPE: U.S.A. California: Siskiyou Co., Shasta Valley, 10 mi. S of Gazelle in gravelly soil at base of hill, ca. 3000 ft., 7 Sep. 1917, *A. A. Heller 12979* [*12579* in protologue] (holotype, GH [barcode] 00037705!; isotypes, CAS [barcode] 00123669 digital image!, F [barcode] 0050290F digital image!, MO-824996 digital image!, NY [barcode] 00169619!, PH [barcode] 00047862!, UC [barcode] 202446 digital image!, US [barcode] 00889366 digital image!, WTU [barcode] 80620 digital image!).

Heads radiate, 2–2.5 cm diam. Ray florets 11 to 28; tube glabrous, ligule linear-elliptic, 5–9 mm, apex entire. Chromosome numbers: $n = 6$ (Dunford, 1986: 303); $2n = 12$ (Whitaker & Steyermark, 1935: 71; Morton, 1981: 361; Cronquist, 1994: 256).

Iconography. Steyermark (1934: 523, fig. 27); Lane (1993: 279).

Distribution and habitat. *Grindelia nana* var. *nana* grows in rocky, sandy, and volcanic soils, on hillsides, from 700 to 750 m, in California, Idaho, Oregon, and Washington (U.S.A.).

Phenology. *Grindelia nana* var. *nana* flowers from June to August.

Common name. Idaho gumweed (<http://plants.usda.gov/>).

Discussion. The characters of *Grindelia brownii* (Heller, 1899: 315) match those of *G. nana* var. *nana*. *Grindelia integerrima*, from Idaho to the east of the coastal distribution of *G. nana*, was differentiated from *G. nana* by its broader phyllaries with shorter tips (Rydberg, 1910: 128), but this fits within the variation observed in *G. nana* var. *nana*.

The names we include in the synonymy of *Grindelia nana* var. *nana* were all considered varieties or forms of *G. nana* by Steyermark in 1934, based on variation among stems, leaves, and the curvature of phyllaries. Nonetheless, we consider that these diverse infraspecies all fall within the variability encompassed by the autonymic variety for *G. nana*.

Taxonomically, Lane (1993) considered *Grindelia nana* var. *altissima* to be a hybrid between *G. nana* var. *nana* and *G. hirsutula* var. *davyi* (= *G. humilis* var. *humilis* in the present paper).

Additional specimens examined. U.S.A. **California:** Plumas Co., Sierra City, *M. S. Taylor 4256* (MO); Siskiyou Co., Shasta, *H. E. Brown 599* (PH), *E. L. Greene 974* (MO). **Idaho:** Kootenai Co., Blackwell's Hill, Coeur d'Alene, *J. H. Christ 11478* (NY). **Oregon:** Wasco Co., 8 mi. W of Wapinita, *J. W. Thompson 4945* (PH); 15 mi. S of Maupin, *J. A. Moore & J. A. Steyermark 3688* (MO); 15 mi. N of Maupin, 10 Aug. 1931, *J. A. Moore & J. A. Steyermark s.n.* (MO-1025977); 8 mi. W of Wapinitia, *J. W. Thompson 4745* (MO). **Washington:** Adams Co., in moist sagebrush slopes near Washtucna, *J. W. Thompson 17376* (PH); Spokane Co., 28 June 1884, *W. N. Suksdorf s.n.* (PH); sandy open ground near Spokane, *E. J. Palmer 37831* (MO); Spokane, Aug. 1898, *T. E. Savage, J. E. Cameron & F. E. Lanoker s.n.* (MO-130040); 3 mi. N of Spangle, *W. A. Weber 2232* (MO).

23b. Grindelia nana var. **columbiana** Piper, Contr. U.S. Natl. Herb. 11: 556. 1906. Replaced name: *Grindelia discoidea* Nutt., Trans. Amer. Philos. Soc. 7: 315. 1840, nom. illeg., non *Grindelia discoidea* Hook. & Arn., Companion Bot. Mag. 2: 45. 1836. *Grindelia nana* Nutt. var. *discoidea* (Nutt.) A. Gray, Syn. Fl. N. Amer. 1(2): 119. 1906, nom. illeg. *Grindelia columbiana* (Piper) Rydb., Bull. Torrey Bot. Club 37: 128. 1910. TYPE: U.S.A. Oregon: Vancouver, *T. Nuttall s.n.* (holotype, PH [barcode] 00047854!; isotype, GH [barcode] digital image!).

Heads discoid. Chromosome number: $2n = 12$ (Cronquist, 1994: 256, sub *Grindelia columbiana* (Piper) Rydb.).

Iconography. Cronquist (1994: 257), sub *Grindelia columbiana*.

Distribution and habitat. *Grindelia nana* var. *columbiana* grows on sandy or gravel soils, along streams, from 30 to 700 m, in Washington and Oregon (U.S.A.).

Phenology. *Grindelia nana* var. *columbiana* has been collected in flower late June to August.

Etymology. The original name of the variety is taken from the Latin "discoideus," which in the Compositae refers to the lack of ligulate florets, with all the florets regular and alike. The replacement name derives from the type locality.

Common name. Columbia River gumweed (<http://plants.usda.gov/>).

Discussion. When Nuttall (1840) described *Grindelia discoidea* he was unaware of the prior blocking name published by Hooker and Arnott four years earlier. It was Piper who offered the replacement name, although he indicated no rank for the trinomial when published in 1906. Gray's use of the infraspecies at the varietal rank is continued herein.

Additional specimens examined. U.S.A. **Oregon:** Portland, dry rocky bluffs, *L. F. Henderson 435* (MO); lowest Albina, *E. P. Sheldon 10960* (MO). **Washington:** Benton Co., Kennewick, *N. Jones 354* (PH); Columbia River shoreline, N of 100-D area, *C. Baird 1397* (NY); Chelan Co., Wenatchee, 26 Sept. 1901, *L. M. Umbach s.n.* (PH); Klickitat Co., Sept. 1883, *W. N. Suksdorf s.n.* (PH); drying up ponds among sagebrush, *J. W. Thompson 11119* (MO); Lincoln Co., sagebrush plains near Wilbur, *J. W. Thompson 7164* (MO, PH); Yakima Co., *J. S. Cotton 780* (MO).

24. Grindelia nelsonii Steyerm., Ann. Missouri Bot. Gard. 21: 471. 1934. TYPE: Mexico. Michoacán: Los Reyes, 8–12 Feb. 1903, *E. W. Nelson 6864* (holotype, US [barcode] 00127644 digital image!; isotypes, GH [barcode] 00008450!, NY [barcode] 00169634 digital image!).

Perennial subshrubs, 0.4–0.5 m; stem 1, erect, ramified, with scattered simple hairs. Leaves herbaceous, sessile, oblong to obovate-elliptic, 1–7.5 × 0.3–1.2 cm, scarcely clasping; blade apex acute to acuminate, margin serrate, teeth ending in a group of sessile glandular trichomes, with scattered sessile glandular trichomes and simple hairs on both blade surfaces. Heads radiate, pedunculate, 3–5 cm diam.; involucre hemispheric-campanulate, moderate to scarcely resinous, 8–13 × 15–25 mm; phyllaries in 4 or 5 subequal series, acuminate, linear-elliptic, 4–9 mm, erect, glabrous; acumen triangular, reflexed, flat, with sessile glandular trichomes; outer phyllaries with acumen very long and narrow. Ray florets 25 to 30; tube glabrous, ligule narrowly elliptic, 17–22 mm, apex entire. Disk florets with corolla 3.5–5.5 mm, with an abruptly ampliate throat. Achenes subquadrate, brown, 2.5–4 mm, smooth or longitudinally striate with shallow transverse incisions at the top, apex truncate or rounded; pappus of 2 or 3 bristles, 4–4.5 mm, smooth. Chromosome number not known.

Iconography. Steyermark (1934: 465, fig. 6).

Distribution and habitat. *Grindelia nelsonii* is known only from the type specimen. It has been collected from Michoacán (Mexico).

Phenology. *Grindelia nelsonii* has been collected in flower in February.

Etymology. *Grindelia nelsonii* was named in honor of Edward William Nelson (1855–1934), an American naturalist and ethnologist who collected in Mexico from 1892 to 1906.

Discussion. *Grindelia nelsonii* is characterized by its large radiate heads (3–5 cm diameter), with acuminate phyllaries in subequal series, the toothed leaves ending in a group of sessile glandular trichomes. This species is similar to a sympatric species, *G. palmeri* Steyerm., with which it shares the marginal teeth of the leaves ending in a group of sessile glandular trichomes, and the broad heads with acuminate phyllaries arranged in subequal series. *Grindelia nelsonii* differs by the long and narrow acumen in the outer phyllaries (equal to or shorter than the base in *G. palmeri*), and the subquadrate, smooth or longitudinally striate achenes with shallow transverse incisions at the apex (vs. 2- or 3-angled, smooth or slightly rugose in *G. palmeri*).

25. Grindelia oaxacana G. L. Nesom, Phytologia 68: 323. 1990. Replaced synonym: *Grindelia micro-*

cephala DC. var. *montana* Steyerm., Ann. Missouri Bot. Gard. 21: 470. 1934. Blocking name: *Grindelia montana* Phil., Anales Univ. Chile 87: 429. 1894. TYPE: Mexico. Oaxaca: Mtns. San Juan del Estado, 7500 ft., 13 Aug. 1894, *L. C. Smith 135* (holotype, GH [barcode] 00008449!; isotype, MEXU-528072 digital image!). Figure 12.

Subshrubs (annual, biannual, or perennial?; see Nesom, 1990), 0.4 m; stem 1, erect, ramified, densely covered by simple hairs and stipitate glandular trichomes. Leaves herbaceous, sessile, oblong-ovate, 2–5 × 0.8–2 cm, clasping, auriculate; blade apex obtuse, margin serrate, teeth blunt, with minute stipitate glandular trichomes on both blade surfaces. Heads radiate, sessile, 1.6–2 cm diam.; involucre hemispheric, resinous, 11–13 × 17–20 mm; phyllaries in 5 or 6 unequal series, graduated, acuminate, oblong-obovate, 2.5–3 mm, erect, glabrous; acumen flat to subterete, erect to strongly reflexed, with sessile glandular trichomes. Ray florets 16 to 22; tube glabrous, ligule narrowly elliptic, 14–16 mm, apex entire. Disk florets with corolla 5 mm, with an abruptly ampliate throat. Immature achenes with transverse incisions, apex truncate; pappus of 2 setiform awns, 4.2–4.5 mm, smooth. Chromosome number not known.

Distribution and habitat. *Grindelia oaxacana* has been collected from mountainous places, ca. 2250 m, in Oaxaca and Puebla (Mexico).

Phenology. *Grindelia oaxacana* has been collected from the beginning of June to August.

Etymology. The name of *Grindelia oaxacana* is taken from the state of Oaxaca, Mexico, where the type specimen was collected.

Discussion. Differentiating characters of *Grindelia oaxacana* include the sessile, radiate heads, with acuminate phyllaries, flat to subterete acumen in graduated series, and clasping, auriculate leaves with minute stipitate glandular trichomes on both surfaces, the marginal teeth with blunt apices. *Grindelia oaxacana* differs from the sympatric species *G. hirtella* and *G. inuloides* by the teeth of the leaves with blunt apices (vs. teeth ending in a sclerotic tip both in *G. hirtella* and *G. inuloides*) and the pappus with two setiform awns (vs. two or three bristles in *G. hirtella* and *G. inuloides*).

Additional specimens examined. MEXICO. **Oaxaca:** Tepelmeme Villa de Morelos, Cerro Verde, Tierra Colorada, *P. Tenorio Lezama 20201* (MEXU). **Puebla:** open fields along rte. 150, ca. 8 mi. E of Puebla, *R. Merrill King 2631* (TEX).

26. Grindelia obovatifolia S. F. Blake, J. Wash. Acad. Sci. 32: 147. 1942. TYPE. Mexico. Nuevo León: Mpio. Montemorelos, abundant throughout pine, oak, & oak–Douglas fir forest, E slope of Sierra de la Cebolla, 21 Aug. 1939, *C. H. Mueller 2932* (holotype, US [barcode] 00127646 digital image!; isotype, GH [barcode] 00008451 digital image!). Figure 13.

Rhizomatous herbs, 0.3–0.5 m; stems 1 or 2, erect, not ramified, glabrous or with simple hairs. Leaves herbaceous, sessile; blade apex obtuse, margin crenate-serrate, teeth blunt indurate or ending in few sessile glandular trichomes, or in a sclerotic tip; basal leaves ovate-elliptic, 4–5 × 2–2.7 cm, blades attenuate into a pseudopetiole as long as the blade, with scattered stipitate glandular trichomes; cauline leaves obovate, 3.5–6 × 1.5–2.8 cm, with simple hairs and stipitate glandular trichomes and scattered sessile glandular trichomes. Heads radiate, pedunculate, 1.3–2.5 cm diam.; involucre hemispheric-campanulate, scarcely resinous, 7–9.5 × 5–7 mm; phyllaries in 5 or 6 unequal series, graduated, acuminate, elliptic, 8–15 mm, spreading, glabrous; acumen subterete, 1.5–2.5 mm, reflexed, with sessile glandular trichomes. Ray florets 17 to 20; tube glabrous, ligule linear-elliptic, 13–14 mm, apex entire. Disk florets with corolla 5–5.6 mm, with a gradually ampliate throat. Achenes elliptic, brownish, flat, 2- or 3-angled, 3–3.5 mm, with transverse incisions, apex truncate; pappus of 2 or 3 bristles, 4.2–4.7 mm, smooth. Chromosome number: $2n = 12$ (Zhao, 1996: 260).

Distribution and habitat. *Grindelia obovatifolia* has been collected from pine, fir, and oak forests, at elevations from 1600 to 2400 m, in Nuevo León (Mexico).

Phenology. *Grindelia obovatifolia* flowers from August to November.

Etymology. The specific epithet is taken from the Latin "obovatus," meaning "obovate," and "folius," meaning "leaved," which refers to the shape of the leaves.

Discussion. *Grindelia obovatifolia* is a quite distinct rhizomatous herb, with the basal leaves with attenuate blades in a pseudopetiole as long as the blade. The heads are radiate with acuminate phyllaries in graduated, five or six series. It differs from *G. robinsonii*, another rhizomatous herb from Mexico, by the pseudopetiolate basal leaves (vs. sessile leaves in *G. robinsonii*) and the presence of stipitate glandular trichomes (vs. the absence of stipitate glandular trichomes in *G. robinsonii*).

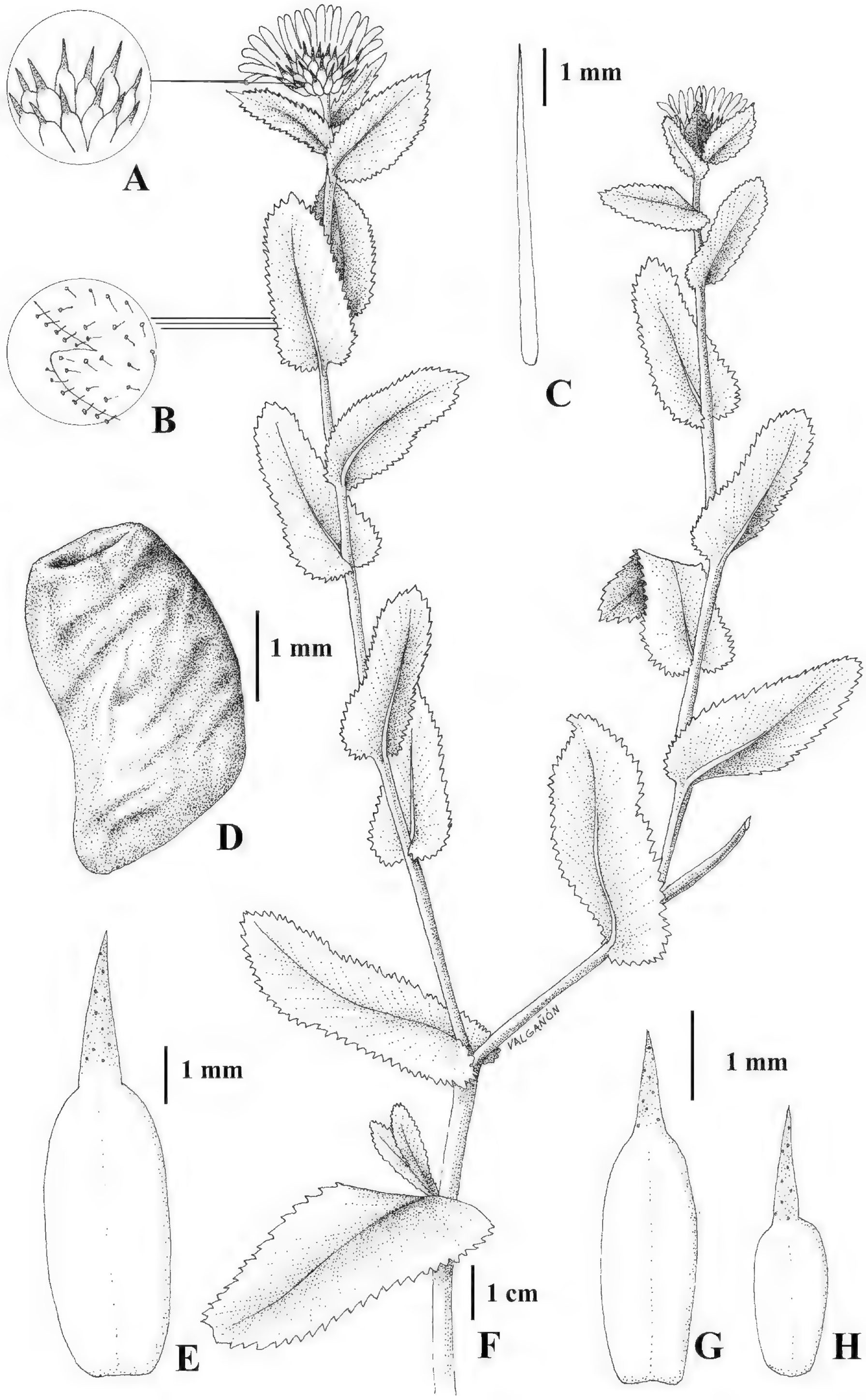

Figure 12. *Grindelia oaxacana* G. L. Nesom. —A. Part of the involucre, inner phyllary series represented. —B. Leaf tooth, showing blunt teeth, with minute stipitate glandular trichomes on both surfaces. —C. Pappus, showing one of two setiform awns. —D. Achene, showing transverse incisions. E, G, H. Representative phyllaries. —E. Inner series. —G. Middle series. —H. Outer series. —F. Fertile habit. Drawn from *R. Merrill King 2631* (TEX).

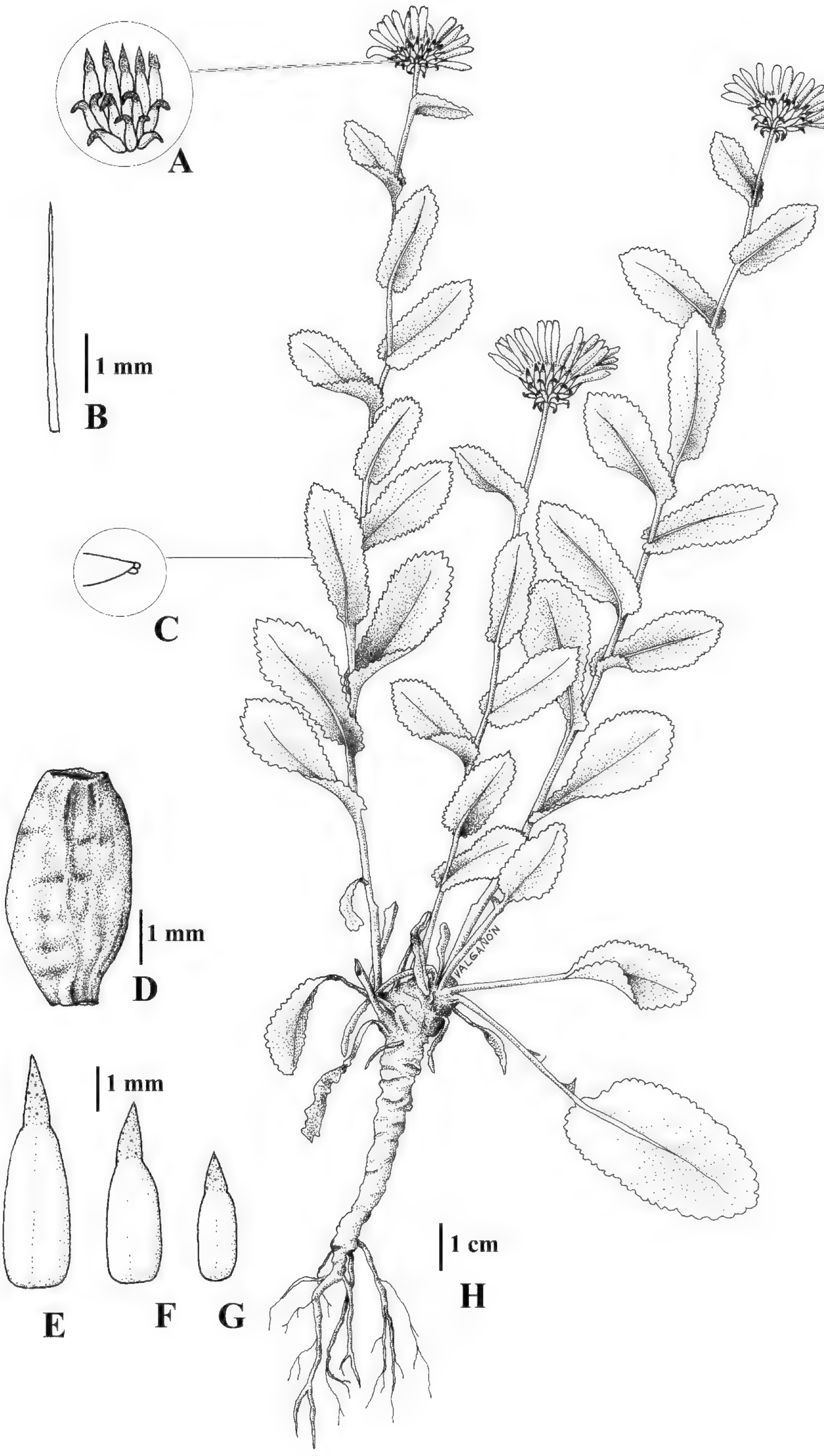

Figure 13. *Grindelia obovatifolia* S. F. Blake. —A. Part of the involucre, inner phyllary series represented. —B. Pappus bristle, showing one of two or three smooth bristles. —C. Leaf tooth, with the apex blunt and indurate or ending in a few sessile glandular trichomes (shown) or in a sclerotic tip. —D. Achene, showing the transverse incisions and two or three angles. E–G. Representative phyllaries. —E. Inner series. —F. Middle series. —G. Outer series. —H. Fertile habit. Drawn from *G. B. Hinton et al. 20024* (TEX).

Additional specimens examined. MEXICO. **Nuevo León:** Mpio. Aramberri, Aramberri, *G. B. Hinton et al. 20024* (TEX); Mpio. Doctor Arroyo, ca. 35 km NE of Doctor Arroyo, along rd. ca. 0.5 mi. S of El Puerto, NE of San Antonio Pena Nevada, NW side of Cerro Peña Nevada, *G. L. Nesom & D. Morgan 6789* (MO); Mpio. Galeana, above El Carrizo, *G. B. Hinton 18618* (MEXU, TEX, XAL); Agua Blanca to San Miguel, *G. B. Hinton et al. 21316* (MEXU); Mpio. Iturbide, Iturbide–Agua Blanca, *G. B. Hinton et al. 21161* (TEX); La Purísima–Bella Vista, *G. B. Hinton 21434* (MEXU, TEX); ca. 25 km S of Iturbide, along rd. 3.3 km W of Ejido La Purísima, *S. Sundberg et al. 1890* (TEX); Mpio. Zaragoza, NW slope of Cerro Peña Nevada, ca. 0.5 rd. mi. below Puerto Pinos, on N side of the peaks, up from San Antonio Pena Nevada, *G. L. Nesom et al. 7086* (TEX); Cerro El Viejo, *G. B. Hinton et al. 2131* (MEXU), *G. B. Hinton et al. 22398* (MEXU); ca. 3 air km. E of Zaragoza, W to WSW of Cerro El Viejo peak on local, *G. L. Nesom et al. 7718* (TEX); Cañón La Boca, camino a Cola de Caballo, Laguna de Sánchez, *J. A. Villarreal et al. 2351* (XAL).

27. Grindelia oolepis S. F. Blake, Proc. Biol. Soc. Washington 41: 139. 1928. TYPE: U.S.A. Texas: Cameron Co., El Jardín to Point Isabel Rd., 10 m, 5 Aug. 1923, *R. Runyon 506* (holotype, US [barcode] 00127647 digital image!; isotype, GH [barcode] 00008434 digital image!).

Rhizomatous perennial herbs, 0.15–0.5 m; stems several, prostrate with tips rising upward erect, single or ramified, glabrous or with simple hairs in the distal portion. Leaves herbaceous, with sessile glandular trichomes on both blade surfaces, sometimes with simple hairs; basal leaves pinnatisect or deeply toothed, 2.5–6 × 0.25–0.7 cm, attenuate into a pseudopetiole; blade apex obtuse, mucronate, teeth ending in a sclerotic tip; cauline leaves sessile, linear to narrowly obovate, 0.7–4 × 0.2–4.5 cm, clasping; blade apex acute, mucronate, margin entire or toothed, teeth ending in a sclerotic tip. Heads discoid, pedunculate; involucre hemispheric to campanulate, resinous, 6–9 × 8–15 mm; phyllaries in 4 or 5 unequal series, graduated, subulate, oblong to ovate, 3–5.5 mm, erect, glabrous, apex flat with sessile glandular trichomes. Disk florets with corolla 4–5 mm, with a gradually ampliate throat. Achenes yellowish or yellow-brown, elliptic, 2- or 3-angled, smooth or somewhat rugose, apex truncate or coronate; pappus of 2 setiform awns or subulate scales, 4–4.5 mm, straight, smooth. Chromosome number: $2n = 12$ (Dunford, 1969: 20).

Iconography. Steyermark (1934: 518, fig. 24).

Distribution and habitat. *Grindelia oolepis* grows on clay soils and grasslands, from 0 to 20 m, in Texas (U.S.A).

Phenology. *Grindelia oolepis* flowers from August to December.

Etymology. The specific epithet is taken from the Latin "oo-," meaning "egg," and from the Greek "lepis," meaning "scale," which refers to the ovate shape of the phyllaries.

Common name. Plains gumweed (<http://hortiplex.gardenweb.com>).

Discussion. *Grindelia oolepis* is a rhizomatous perennial herb immediately distinguished from all other herbaceous species of the genus with its pinnatisect or deeply toothed basal leaves, and discoid heads with subulate phyllaries in graduated, four or five series.

Additional specimens examined. U.S.A. **Texas:** Cameron Co., Brownsville, 14 Nov. 1933, *R. Runyon & J. A. Steyermark s.n.* (MO-2762590); SE corner of 1 E and St. Francis, *M. A. Wetter 737* (MO); W end of Palm Blvd., Brownsville, *V. L. Cory 51421* (GH); Jim Wells Co., 3 mi. W of Nueces–Jim Wells Co. line W of Agua Dulce, *M. A. Wetter 2035* (NY); Nueces Co., Agua Dulce, *B. C. Tharp 44451* (MO); near Agua Dulce, *M. A. Wetter 738* (MO); ca. 1/4 mi. S of St. Paul on Hwy. 181, *W. F. Mahler 8653* (GH); San Patricio Co., Hwy. 234 betw. Odem & Edray, *M. P. Dunford & C. E. Freeman 1156* (NY).

28. Grindelia oxylepis Greene, Pittonia 4: 42. 1899. TYPE. Mexico. Chihuahua: wet places, plains near Chihuahua, 17 Sep. 1886, *C. G. Pringle 748* (holotype, NDG-53620 digital image!; isotypes, BRIT-23676 digital image!, E [barcode] 00385585 digital image!, GH [barcode] 00008452 digital image!, MICH [barcode] 1107422 digital image!, MO-193878!, NY [barcode] 169636 digital image!, NY [barcode] 169637 digital image!, PH [barcode] 47864 digital image!, RSA [barcode] 0001226 digital image!, US [barcode] 00056850 digital image!, US [barcode] 01417150 digital image!).

Grindelia oxylepis Greene f. *capitellata* Steyerm., Ann. Missouri Bot. Gard. 21: 490. 1934, syn. nov. TYPE: Mexico. Durango: Mapimi & vic., 21–23 Oct. 1898, *E. Palmer 520* (holotype, GH [barcode] 00008453!; isotypes, MO-193820!, NY [barcode] 169638 digital image!, US [barcode] 00127650 digital image!).

Annual or biannual subshrubs, 0.2–0.55 m; stems 1, rarely 2, erect, ramified, glabrous. Leaves subcoriaceous, sessile, oblong or obovate, 1–3 × 0.3–0.8 cm, clasping; blade apex obtuse, margin minutely serrate, teeth blunt or ending in a group of sessile glandular trichomes, less commonly spinulose, with sessile glandular trichomes in pits on both surfaces. Heads radiate, short pedunculate, 1.5–2 cm diam.; involucre urceolate, resinous, 7–10 × 8–16

mm; phyllaries in 4 or 5 unequal series, strongly graduated, subulate, narrowly elliptic, 4–8 mm, apex flat to subterete, mucronate, with sessile glandular trichomes in pits; the outer bracts spreading; the middle phyllaries and the upper erect. Ray florets 20 to 30; tube glabrous, ligule narrowly obovate, 7–9 mm, apex entire. Disk florets with corolla 4–6 mm, with an abruptly ampliate throat. Achenes brown, subquadrate, 1.5–3 mm, tuberculate, apex truncate or with a crown; pappus of 2 or 3 setiform awns, 4–6 mm, straight, smooth to barbellate. Chromosome number: $2n = 12$ (Semple et al., 1989: 302).

Iconography. Steyermark (1934: 495, fig. 13).

Distribution and habitat. *Grindelia oxylepis* grows on sandy and clay soils, in valleys and plains, from 800 to 1600 m, in Chihuahua, Coahuila, Durango, and San Luis Potosí (Mexico).

Phenology. *Grindelia oxylepis* flowers from April to November.

Etymology. The specific epithet is taken from the Greek "oxi-," for "acute," and "-lepis," for "scale," which refers to the mucronate apex of the phyllaries.

Common name. Mexican gumweed (<http://hortiplex.gardenweb.com>; <http://data.gbif.org/species/13765388>).

Discussion. *Grindelia oxylepis* is an annual or biannual subshrub, characterized by its radiate heads with an urceolate involucre and with subulate phyllaries in a strongly graduated, four or five series. *Grindelia oxylepis* f. *capitellata* was established by Steyermark (1934: 490) out of consideration for the smaller heads, noted as "campanulate-hemispherical to campanulate, 0.5–0.7 cm. high, 0.5–0.7 cm. in anthesis, becoming 1–1.3 cm. broad in fruit." There does seem to be continuous variation for this character in *G. oxylepis*. We did study two specimens annotated as the form from the type locality in Durango (Bolsón de Mapimí: *J. Gregg 444* and *J. Gregg 627*, MO), with heads that were equal in diameter to those seen in the species type.

Additional specimens examined. MEXICO. **Chihuahua:** Ahumada, in wet ditch along trail, *J. Henrickson 5802a* (TEX); Meoqui, *D. H. LeSueur 974* (MO, TEX); 1 mi. S of Villa Ahumada along Chihuahua hwy. 45, 1/2 mi. E of hwy., *R. Spellenberg et al. 4042* (TEX). **Coahuila:** Saltillo, rancho demostrativo Los Ángeles, 48 km S de Saltillo, *D. G. Arredondo 227* (XAL); 25.4 mi. NW of San Pedro, in wet roadside ditch area, *J. Henrickson 5988* (NY); Torreón, *L. Fisher 44165* (MO); plains near Filipinas, *C. A. Purpus 4701* (MO); General Cepeda, Presa El Tulillo, 9 km carr. a Hipólito del entronque carr. Saltillo–Torreón, *J. A. Villarreal & M. A. Carranza 2312* (TEX, XAL). **Durango:** Bolsón de Mapimí, *J. Gregg 444* (MO); valley of Nazas, Bolsón de Mapimí, *J. Gregg 627* (MO); old cornfields at city of Durango & vic., *E. Palmer 174* (MO). **San Luis Potosí:** 1879, *J. G. Schaffner 738* (NY); ca. 7 mi. N of San Luis Potosí on hwy. 57, *R. C. Jackson 5097* (TEX); 8.7 mi. N of San Luis Potosí, *R. Kral 27380* (MO); Mpio. Villa Hidalgo, ca. 20 mi. NW of San Luis Potosí on hwy. 57 to Matehuala, 9.8 mi. S of RR crossing at Ventura, *G. L. Nesom 6660 with J. Wells* (TEX).

29. Grindelia palmeri Steyerm., Ann. Missouri Bot. Gard. 21: 471. 1934, as "Palmeri." TYPE: Mexico. San Luis Potosí: Álvarez, 28 Sep.–3 Oct. 1902, *E. Palmer 163* (holotype, US [barcode] 00127652 digital image!; isotypes, BM [barcode] 001009430 digital image!, F [barcode] 0050297F digital image!, GH [barcode] 00008455!, MEXU-33213 digital image!, MO-193819!, NY [barcode] 00169640!).

Perennial shrubs, 0.1–0.5 m; stems 1 to 4, ascendent to erect, ramified, with scattered simple hairs, but villous near the heads. Leaves herbaceous, sessile, broadly oblong to obovate-elliptic, 1–7.5 × 0.3–1.5 cm, base somewhat subcordate, clasping; blade apex acute to obtuse, margin crenate-serrate, teeth ending in a few sessile glandular trichomes, simple hairs occasionally present near the nerves, scattered sessile glandular trichomes on both surfaces; cauline leaves progressively smaller. Heads radiate, pedunculate, 3–5 cm diam.; involucre hemispheric-campanulate, scarcely resinous, 8–13 × 15–25 mm; phyllaries in 4 or 5 subequal series, acuminate, linear-elliptic, erect, 4–9 mm, glabrous; acumen triangular, flat, reflexed, with sessile glandular trichomes; outer phyllaries with acumen equal to or shorter than base. Ray florets 25 to 35; tube glabrous, ligule narrowly elliptic, 10–22 mm, apex entire. Disk florets with corolla 3.5–5.5 mm, with an abruptly ampliate throat. Achenes yellowish brown or brown, elliptic, 2- or 3-angled, smooth or slightly rugose, apex truncate or rounded; pappus of 2 or 3 bristles, 4.5–5.5 mm, smooth. Chromosome number not known.

Iconography. Steyermark (1934: 465, fig. 8).

Distribution and habitat. *Grindelia palmeri* has been collected in oak, pine, and acacia forests, from 150 to 2500 m in Colima, Michoacán, and San Luis Potosí (Mexico).

Phenology. *Grindelia palmeri* has been collected in flower from July to October.

Etymology. *Grindelia palmeri* was named in honor of Edward Palmer (1829–1911), a British botanist who participated in the 1891 expedition to

Death Valley, California. He also collected specimens in Mexico and South America.

Common name. Cabezona (<http://www.thepanamanews.com/pn/v_08/issue_18/science_02.html>).

Discussion. *Grindelia palmeri* is a species with large radiate heads 3–5 cm in diameter, with the acuminate phyllaries in subequal, four or five series; the acumen of the phyllaries is triangular, flat, and reflexed, and the achenes are elliptic, 2- or 3-angled, and smooth or slightly rugose. It is similar to *G. nelsonii*, sharing the size of the heads, the arrangement of the phyllaries, and the pappus with two or three bristles. *Grindelia palmeri* differs by the form of the acumen of the outer phyllaries (vs. very long and narrow in *G. nelsonii*) and the achenes (vs. subquadrate, smooth or longitudinally striate, with transverse incisions at the apex in *G. nelsonii*).

Additional specimens examined. MEXICO. **Colima:** 3 km S of Michoacán–Colima border, *D. Burch 5139* (MO). **Michoacán:** pasture, ca. 24 rd. mi. W of Jiquilpan, *A. Cronquist 9759* (MO). **San Luis Potosí:** 22°N, *C. C. Parry & E. Palmer 371* (MO); Mpio. Zaragoza, slopes, 10 km W of Santa Catarina on Mexican Hwy. 70, *D. E. Breedlove 59348 with F. Almeda* (TEX); microwave hill of Rte. 70 E of San Luis Potosí, W of Santa Catarina, *D. J. Loockerman 40015 with J. A. Soule* (TEX); 33 km E of San Luis Potosí or 1 km of Puerto de la Huerta on Hwy. 86, *K. Roe, E. Roe & S. Mori 144* (TEX).

30. Grindelia paysonorum H. St. John, Res. Stud. State Coll. Wash. 1(2): 108–109. 1929, as "Paysonorum." *Grindelia nana* Nutt. var. *paysonorum* (H. St. John) Steyerm., Ann. Missouri Bot. Gard. 21: 547. 1934. TYPE: U.S.A. Idaho: Nez Perce Co., dry ground, 900 ft., Lime Point, 9 May 1926, *H. St. John 4361* (holotype, WS-48552!; isotype, RM [barcode] 0001124 digital image!).

Grindelia howellii Steyerm., Ann. Missouri Bot. Gard. 21: 549. 1934, as "Howellii." Syn. nov. TYPE: U.S.A. Idaho: Kootenai Co., on dry arid bluff tops, St. Maries River, 10 Aug. 1894, *L. F. Henderson 2791* (holotype, GH [barcode] 00037697!; isotypes, RM [barcode] 0001122 digital image!, RM [barcode] 0001122a digital image!, US [barcode] 00008208 digital image!).

Perennial subshrubs, 0.6–0.9 m; stems 1 or 2, erect, ramified, with stipitate glandular trichomes on the distal portion. Leaves herbaceous, sessile, oblong or elliptic, spatulate, 2.5–7 × 0.7–2.2 cm, base cuneate, somewhat clasping; blade apex acute to obtuse, margin entire, serrate or denticulate, teeth ending in a sclerotic tip, stipitate and sessile glandular trichomes present on both surfaces. Heads radiate, pedunculate to subsessile, 2.5–3 cm diam.; involucre hemispheric-campanulate, resinous, 8–15 × 12–20 mm; phyllaries in 6 or 7 unequal series, graduated, acuminate, elliptic to linear-elliptic, 3.5–10 mm, erect or spreading; acumen subterete, 2–4 mm, in the upper phyllaries revolute to reflexed, with sessile glandular trichomes. Ray florets 20 to 30; tube glabrous, ligule narrowly elliptic, 8–12 mm, apex entire. Disk florets with corolla 6–7 mm, with a gradually ampliate throat. Achenes whitish to yellow, elliptic, 4-angled, 4–4.5 mm, rugose or striate, with a crown at the apex; pappus of 2 to 5 setiform awns, 2.5–4 mm, straight to curved, smooth to barbellulate. Chromosome number not known.

Iconography. Steyermark (1934: 540, fig. 30), sub *Grindelia howellii*.

Distribution and habitat. *Grindelia paysonorum* grows on disturbed soils, grasslands, open forests, and dry hillsides, from 900 to 1500 m, in Idaho and Montana (U.S.A.).

Phenology. *Grindelia paysonorum* has been collected in flower from July to September.

Etymology. The species was named in honor of Edwin Blake Payson (1893–1927), a botanist and professor of botany at the University of Wyoming (U.S.A.).

Discussion. Diagnostic features of *Grindelia paysonorum* include the radiate heads, the acuminate phyllaries, in graduated, six or seven series, the somewhat clasping leaves, with stipitate and sessile glandular trichomes scattered across both blade surfaces. *Grindelia howellii* closely corresponds to these characters, also described from Idaho.

Additional specimens examined. U.S.A. **Idaho:** Benewah Co., breaks of St. Maries River, *S. J. Brunsfeld 79438* (NY); Idaho Co., at top of grade going down to Kamiah from Winona, *Q. Jones 277* (NY); Lemhi Co., Salmon, *P. Edwin B. & L. B. Payson 1883* (MO). **Montana:** Missoula Co., Holland Lake Rd., *J. R. Pierce 1146* (NY); Powell Co., Ovando Valley, common along high water line of glacial ponds on Bandy Ranch SW of Upsata Lake, *P. Lesica 5789* (NY); Greenough, 1 mi. E of Patonic turnoff, disturbed site, *J. R. Pierce 1120* (MO).

31. Grindelia pusilla (Steyerm.) G. L. Nesom, Phytologia 73(4): 327. 1992. Basionym: *Grindelia microcephala* DC. var. *pusilla* Steyerm., Ann. Missouri Bot. Gard. 21: 467. 1934. TYPE: U.S.A. Texas: betw. Frio & Nueces Rivers, on rd. to Laredo, 27/28 Jan. 1880, *E. Palmer 469* (holotype, GH [barcode] 00008433!; isotypes, MO-126251 digital image!, NY [barcode] 00169617!, US [barcode] 00127643 digital image!). Figure 14.

Annual subshrubs, 0.08–0.15 m; stems 1 to 7, erect, ramified, with simple hairs and stipitate glandular trichomes. Leaves herbaceous, elliptic, spatulate, blade apex acute or obtuse, margin crenate, teeth ending in a group of sessile glandular trichomes, with stipitate glandular trichomes and sessile glandular trichomes on both surfaces, occasionally in pits; basal leaves 3.5–6 × 0.5–1 cm, attenuate into a pseudopetiole; cauline leaves 1.2–1.5 × 0.3–0.5 cm. Heads radiate, pedunculate, 0.8–1.5 cm diam.; involucre hemispheric, resinous, 8–12 × 8–13 mm; phyllaries in 4 to 6 subequal series, subulate, the outer and middle narrowly ovate, erect or spreading, 8–10 mm, apex flat, erect or curved, 1.5–2 mm; the upper narrowly elliptic, 12 mm, erect. Ray florets 13 to 27; tube glabrous, ligule elliptic or ovate, 5–12 mm, apex entire or toothed. Disk florets with corolla 4–5 mm, with a gradually ampliate throat. Achenes stramineous to brown, obconic, 2- or 3-angled, 3–4.5 mm, sharply cut with transverse furrows, apex with a crown; the inner flattened; pappus of 2 or 3 setiform awns, 4–5.5 mm, straight, smooth. Chromosome number: $2n = 12$ (Zhao & Turner, 1993: 650).

Distribution and habitat. *Grindelia pusilla* has been collected on dry soils, in disturbed places, from 0 to 500 m, in Texas (U.S.A.) and Coahuila (Mexico).

Phenology. *Grindelia pusilla* flowers from March through June.

Etymology. The specific epithet is taken from the Latin "pusillus," meaning "very small," which refers to the size of the plants.

Common name. Little gumweed (<http://plants.usda.gov/>).

Discussion. We agree with Nesom (1992) in considering *Grindelia pusilla* a different taxon from *G. microcephala*, although both have smaller radiate heads less than 1.5 cm in diameter. *Grindelia pusilla* differs by its 2- or 3-angled, obconic achenes, sharply cut with transverse furrows (vs. 3- or 4-angled, globose achenes with smooth or slightly rugose surfaces in *G. microcephala*).

Additional specimens examined. U.S.A. **Texas:** Denton Co., Clear Creek Natl. Heritage Center, Collins Rd., Rocking Trail, s.d., *S. D. Lusk s.n.* (BRIT-24535); Lasalle Co., Cotulla, *E. J. Palmer 11295* (NY); Uvalde Co., 2 mi. W of Uvalde, rd. 90, *K. Bremer 2325* (MO).

32. Grindelia robinsonii Steyerm., Ann. Missouri Bot. Gard. 21: 459. 1934, as "Robinsonii." TYPE: Mexico. San Luis Potosí: Agua del Medio, July 1911, *C. A. Purpus 5722* (holotype, US [barcode] 00127655 digital image!; isotypes, BM [barcode] 001009431 digital image!, F [barcode] 0050298F digital image!, GH [barcode] 00008456 digital image!, MO-130322 digital image!, NY [barcode] 00169641!).

Rhizomatous perennial herbs, 0.15–0.55 m; stems 1, occasionally 2, erect, single or ramified, with vitreous simple hairs. Leaves subcoriaceous, sessile, oblong to oblong-elliptic, 1–5 × 0.3–1.3 cm, clasping; blade apex obtuse, margin crenate-serrate to minutely serrate, teeth ending in a sclerotic tip, simple hairs and scattered sessile glandular trichomes on both surfaces. Heads radiate, pedunculate, 1.6–2 cm diam.; involucre campanulate, resinous, 7–10 × 10–16 mm; phyllaries in 4 unequal series, strongly graduated, acuminate, linear to oblong-elliptic, 3–6.5 mm, glabrous; the outer bracts reflexed; the middle and the upper phyllaries spreading or erect; acumen subterete, erect, 1–2 mm, with sessile glandular trichomes. Ray florets 15 to 20; tube glabrous, ligule linear-elliptic, 5–7 mm, apex entire. Disk florets with corolla 4–4.5 mm, with an abruptly ampliate throat. Achenes light brown, subquadrate, 2.5–2.6 mm, slightly rugose, apex truncate; pappus of 2 to 5 bristles, 4–4.5 mm, smooth. Chromosome numbers: $n = 6$ (Powell & Turner, 1963: 135); $2n = 12$ (Zhao, 1996: 260).

Iconography. Steyermark (1934: 457, fig. 3).

Distribution and habitat. *Grindelia robinsonii* grows in pine and oak forests, and in grasslands with acacia, at ca. 2300 m in Hidalgo and San Luis Potosí (Mexico) (Nesom, unpublished).

Phenology. *Grindelia robinsonii* has been collected in flower from July to August.

Etymology. *Grindelia robinsonii* was named in honor of Benjamin Lincoln Robinson (1864–1935), curator of the Gray Herbarium at Harvard University and editor of the *Synoptical Flora of North America*, published in 1895–1897.

Discussion. *Grindelia robinsonii* is a rhizomatous herb characterized by its small radiate heads with strongly graduated acuminate phyllaries, in four series, with the outer phyllaries reflexed and a subterete acumen. Among rhizomatous herbs with radiate heads, *G. robinsonii* is similar to *G. obovatifolia* (from Nuevo León, Mexico), with which it shares small heads. *Grindelia robinsonii* differs by its leaves, which are sessile and have marginal teeth that end in a sclerotic tip (vs. attenuate basal leaves with a pseudopetiole as long as the blade, with marginal teeth that end in sessile glandular trichomes, as in *G. obovatifolia*). The achenes are

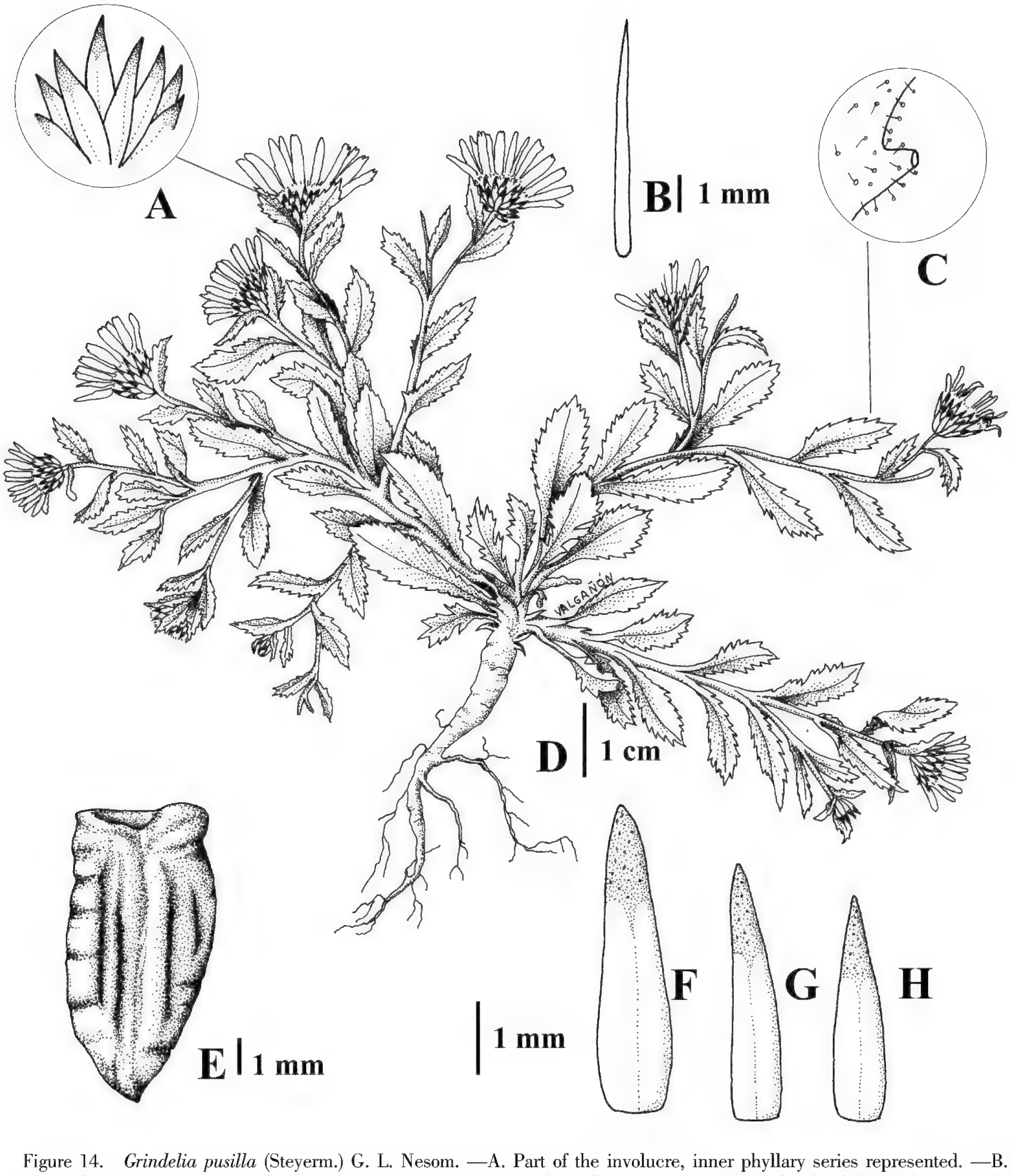

Figure 14. *Grindelia pusilla* (Steyerm.) G. L. Nesom. —A. Part of the involucre, inner phyllary series represented. —B. Pappus, showing one of two or three setiform awns. —C. Leaf tooth, ending in a group of sessile glandular trichomes, with stipitate glandular trichomes and sessile glandular trichomes. —D. Fertile habit. —E. Achene, showing two or three angles. F–H. Representative phyllaries. —F. Inner series. —G. Middle series. —H. Outer series. Drawn from *K. Bremer 2325* (MO).

subquadrate and slightly rugose in *G. robinsonii*, but are elliptic, flat, and 2- or 3-angled, with transverse incisions in *G. obovatifolia*.

Additional specimens examined. MEXICO. **Hidalgo:** Hidalgo, pine woods, *V. H. Chase 7376 1/2* (MO); dry bank of irrigating ditch, *V. H. Chase 7266* (MO); Mpio. Jacala, *L. Fisher 37145* (TEX). **San Luis Potosí:** Minas de San Rafael, *C. A. Purpus 5151* (GH).

33. Grindelia scabra Greene, Bull. Torrey Bot. Club 25: 120. 1898. TYPE: U.S.A. New Mexico: Lincoln Co., White Mtns., 6300 ft., 28 July 1897, *E. O. Wooton 224* (lectotype, designated by Nesom [1990: 320], NDG 53647 digital image!; isolectotypes, MO-714081!, NDG-53648 digital image, NY [barcode] 00169622 digital image!, NY [barcode] 00169624 digital

image!, RM [barcode] 0001127 digital image!, RSA [barcode] 0001228 digital image!, US [barcode] 0030448 digital image!).

Grindelia neomexicana Wooton & Standl., Contr. U.S. Natl. Herb. 16: 178. 1913, syn. nov. *Grindelia scabra* Greene var. *neomexicana* (Wooton & Standl.) Steyerm., Ann. Missouri Bot. Gard. 21: 510. 1934. *Grindelia arizonica* A. Gray var. *neomexicana* (Wooton & Standl.) G. L. Nesom, Phytologia 68(4): 318. 1990. TYPE: U.S.A. New Mexico: mtns. N of Santa Rita, 23 Aug. 1900, *E. O. Wooton s.n.* (holotype, US [barcode] 00561099 digital image!).

Perennial subligneous herbs, 0.2–0.7 m; stems 1 to 4, erect, ramified, glabrous or with simple hairs. Leaves herbaceous, sessile, blade apex obtuse or acute, margin serrate or denticulate, teeth ending in a sclerotic tip, with short simple hairs and sessile glandular trichomes on both surfaces; basal leaves broadly elliptic to oblong-spatulate, 4–8.5 × 2–2.5 cm, attenuate into a pseudopetiole; blade apex obtuse to acute; cauline leaves ovate-oblong to elliptic, 3–3.5 × 1–1.5 cm, clasping; blade apex acute. Heads radiate, sessile, 2–4 cm diam.; involucre hemispheric, resinous, 7–11 × 10–20 mm; phyllaries in 4 to 6 subequal series, acuminate, linear, 7–11 mm, erect or spreading, margin scabrous; acumen filiform, terete or subterete, 2.5 mm, erect, with sessile glandular trichomes. Ray florets 17 to 30; tube glabrous, ligule narrowly elliptic, 12–17 mm, apex entire. Disk florets with corolla 6–7 mm, with a gradually ampliate throat. Achenes light brown, elliptic, 3- or 4-angled, 2.5–3 mm, smooth or slightly striate, apex obliquely truncate or forming a crown; pappus of 2 to 4 bristles, 4–6 mm, smooth to barbellulate. Chromosome number: $2n = 12$ (Dunford, 1986: 302).

Iconography. Greene (1898a: 120, figs. 1, 2).

Distribution and habitat. *Grindelia scabra* grows in plains and rocky hills, from 1400 to 2800 m, in New Mexico and Texas (U.S.A.).

Phenology. *Grindelia scabra* flowers from June to September.

Etymology. The specific epithet is taken from the Latin "scaber," meaning "rough," which refers to the pubescence of the leaves.

Common name. Rough gumweed (<http://hortiplex.gardenweb.com>).

Discussion. Useful characters for distinguishing *Grindelia scabra* include the radiate heads; the acuminate phyllaries with scabrous margins in subequal series; the phyllaries with a filiform acumen; and the leaves with marginal teeth that end in a sclerotic tip.

Nesom (1990) considered *Grindelia neomexicana* a variety of *G. arizonica*, and Strother and Wetter (2006) included this in the synonymy of *G. arizonica*. Nevertheless, the type of *G. neomexicana* corresponds with the diagnostic characters of *G. scabra*. Further, in the species-level taxon *G. arizonica*, the phyllaries have a flat acumen and are arranged in graduated series (vs. subequal in *G. scabra*). Thus, we agree with Steyermark in including *G. neomexicana* in the synonymy of *G. scabra*.

Additional specimens examined. U.S.A. **New Mexico:** Grant Co., Fort Bayard Watershed, *J. C. Blumer 4* (GH); Black Range W flank of Sawyer's Peak, Silver Canyon, around Mitchell Gray's cabin, 20 Aug. 1915, *H. A. Pilsbry s.n.* (PH-574225); Grant-Sierra Co., boundary betw. Sawyer's Peak & Hillsboro Peak, 10 Oct. 1916, *H. A. Pilsbry s.n.* (PH-574223); Lincoln Co., White Mtns., *E. O. Wooton 372* (syntype for *Grindelia neomexicana* NY [barcode] 00169623, RSA [barcode] 0001229, TEX [barcode] 00373595); Otero Co., along US 82 just opposite entrance to Cloud Country Club Estates, *M. A. Wetter 590* (NY); Sierra Co., Kingston, *O. B. Metcalfe 1302* (GH); along NM 90, *C. C. Freeman & M. A. Wetter 2137* (NY). **Texas:** Jeff Davis Co., Davis Mtns., dry rocky ground on ridge above Little Ajuga Canyon, *J. A. Moore & J. A. Steyermark 3043* (MO).

34. Grindelia squarrosa (Pursh) Dunal, Mém. Mus. Hist. Nat. 5: 50. 1819. Basionym: *Donia squarrosa* Pursh, Fl. Amer. Sept. (Pursh) 2: 559. 1814. TYPE: U.S.A. South Dakota: prairies in camp near old Maha village, 17 Aug. 1804, *M. Lewis 40* (holotype, PH [barcode] 00047865!).

Biannual or perennial subshrubs, 0.15–1 m; stems 1 to several, erect or decumbent at the base, ramified, glabrous or with simple hairs. Leaves subcoriaceous; blade apex acute or obtuse, with sessile glandular trichomes in pits on both surfaces; basal leaves entire to pinnatisect, 6–8 × 1.5–2 cm, attenuate into a pseudopetiole; blade apex acute to obtuse, teeth acute and ending in a group of sessile glandular trichomes; cauline leaves sessile, oblong, elliptic, or obovate, 2.5–5 × 0.25–2 cm, clasping, auriculate or subauriculate; blade apex acute to obtuse, margin entire, crenate-serrate, serrate, or denticulate, teeth rounded to obtuse ending in a group of sessile glandular trichomes. Heads radiate or discoid, pedunculate; involucre broadly urceolate to hemispheric, resinous, 6–20 × 8–28 mm; phyllaries in 4 to 6 series, strongly graduated, acuminate, linear-elliptic to narrowly ovate, 4–12 mm, spreading or reflexed; acumen linear to narrowly triangular, terete to subterete, erect to spreading, 4 mm, with sessile glandular trichomes in pits. Disk florets with corolla 4–6 mm, with a gradually ampliate throat. Achenes brownish, 3- or 4-angled, elliptic, 2.5–3 mm, smooth, rugose, or slightly furrowed, apex truncate;

pappus of 2 or 3 setiform awns, curved, 3–5.5 mm, smooth to barbellulate.

Etymology. The specific epithet is taken from the Latin "squarrosus," meaning "rough, with scales, tips, or bracts projecting outward at about 90°," which refers to the spreading or reflexed phyllaries.

Discussion. *Grindelia squarrosa* is characterized by its acuminate phyllaries in graduated series and by its leaves with sessile glandular trichomes in pits on both surfaces and marginal teeth that end in a group of sessile glandular trichomes. The taxon is similar to *G. subdecurrens* by the leaves that bear sessile glandular trichomes in pits on both surfaces, and the marginal teeth that end in a group of sessile glandular trichomes; the heads in both species have acuminate phyllaries arranged in four to six strongly graduated series. However, *G. squarrosa* differs by its achene surfaces being smooth, rugose, or slightly furrowed (achenes have prominent longitudinal furrows in *G. subdecurrens*) and the pappus with curved, setiform awns (a pappus of two to four straight bristles in *G. subdecurrens*).

Three varieties and two forms are recognized within *Grindelia squarrosa*. The three varieties are distinguished in the key couplets below, with the forms considered under the autonymic variety.

1a. Heads radiate ..... 34a. *G. squarrosa* var. *squarrosa*
1b. Heads discoid.
  2a. Involucre 8 mm broad ..... 34b. *G. squarrosa* var. *eligulata*
  2b. Involucre 15–20 mm broad ..... 34c. *G. squarrosa* var. *nuda*

34a. Grindelia squarrosa var. **squarrosa.**

Heads radiate, 2.2–3.3 cm diam. Ray florets 22 to 36, tube glabrous, ligule narrowly elliptic, 7–15 mm, apex entire. Achenes smooth or rugose.

Two forms are further distinguished in the couplet below.

1a. All leaves entire ... 34a(1). *G. squarrosa* f. *squarrosa*
1b. Basal leaves pinnatisect ..... 34a(2). *G. squarrosa* f. *pseudopinnatifida*

34a(1). Grindelia squarrosa f. **squarrosa.**

Grindelia perennis A. Nelson, Bull. Torrey Bot. Club 26: 355. 1899, syn. nov. TYPE: U.S.A. Wyoming: Sweetwater River, 27 July 1898, *A. Nelson 4988* (holotype, RM [barcode] 0001126 digital image!; isotypes, MO [barcode] 714079 digital image!, NY [barcode] 00169621!, UTC-171663 digital image!).

Grindelia serrulata Rydb., Bull. Torrey Bot. Club 31: 646. 1904, syn. nov. *Grindelia squarrosa* (Pursh) Dunal var. *serrulata* (Rydb.) Steyerm., Ann. Missouri Bot. Gard. 21: 482. 1934. TYPE: U.S.A. Colorado: Ft. Collins, 5000 ft., 10 Aug. 1891, *J. M. Cowen s.n.* (holotype, NY [barcode] 169625!).

Grindelia squarrosa (Pursh) Dunal var. *quasiperennis* Lunell, Amer. Midl. Naturalist 3: 143. 1913, syn. nov. TYPE: U.S.A. North Dakota: Butte, 2 Aug. 1909, *J. Lunell 1040* (lectotype, designated by Cronquist [citing annotated by Mark Wetter, 1994: 256], MIN not seen).

Grindelia squarrosa (Pursh) Dunal f. *depressa* Steyerm., Ann. Missouri Bot. Gard. 21: 480. 1934, syn. nov. TYPE: U.S.A. Utah: alkali flat, 5 mi. W of Salt Lake City, 1300 m, 23 Aug. 1931, *J. A. Moore & J. A. Steyermark 3768* (holotype, MO-1027218!).

Leaves entire with blade margin nearly entire, sharply toothed or denticulate. Chromosome numbers: $n = 6$ (Pinkava & Keil, 1977: 681, sub *Grindelia squarrosa* var. *serrulata*; Lane & Li, 1993: 542, sub *G. squarrosa* var. *serrulata*); $2n = 12$ (Morton, 1981: 361; Cronquist, 1994: 256).

Iconography. Cronquist (1994: 259).

Distribution and habitat. *Grindelia squarrosa* f. *squarrosa* grows on disturbed sandy soils, prairies, hillsides, and along streams, from 200 to 2900 m, in Arkansas, Colorado, Indiana, Iowa, Kansas, Massachusetts, Michigan, Montana, Nebraska, New Jersey, North Dakota, Pennsylvania, South Dakota, Texas, Utah, Wisconsin, and Wyoming (U.S.A.) and Coahuila (Mexico).

Phenology. *Grindelia squarrosa* f. *squarrosa* flowers from July to September.

Common name. Curly cup gumweed (<http://hortiplex.gardenweb.com>; <http://plants.usda.gov/>).

Discussion. In *Grindelia squarrosa* f. *squarrosa* the leaves and margin of the blade are variable in shape. *Grindelia perennis*, with slender, nearly entire leaves (Nelson, 1899: 356), and *G. serrulata*, with sharply toothed leaves (Rydberg, 1904: 646), share the diagnostic characters of *G. squarrosa*. The same is accepted for the variety *quasiperennis* with denticulate leaves that narrow toward the base (Lunell, 1913: 143), which was included in the synonymy of *G. perennis* by Steyermark.

Fitting within the taxonomic variation encompassed by *Grindelia squarrosa*, variety *quasiperennis*, variety *serrulata*, and form *depressa* established by Steyermark (1934) are included in the synonymy of *G. squarrosa* var. *squarrosa*, within form *squarrosa*.

Strother and Wetter (2006) considered *Grindelia perennis* a synonym of *G. hirsutula*. Nevertheless, the type of *G. perennis* matches the diagnostic characters of *G. squarrosa* and differs from *G. hirsutula* in its acuminate phyllaries (vs. subulate in *G. hirsutula*), its

sessile glandular trichomes in pits on the leaves (vs. scattered and not in pits in *G. hirsutula*), and its leaves with marginal teeth terminated by a group of sessile glandular trichomes (vs. the sclerotic tip seen in *G. hirsutula*).

Additional specimens examined. U.S.A. **Arkansas:** sandy banks of Arkansas River, 20 mi. above Little Rock, *G. Engelmann 650* (MO). **Colorado:** Chaffee Co., 12 mi. W of Salida, *J. A. Moore & J. A. Steyermark 3781* (MO). **Indiana:** Lagrange Co., SE Ontario, *C. D. Chas 36* (PH). **Iowa:** Sioux Co., sandy margin of Rock River, *J. L. Carter 1961* (PH); Lee Co., dry ground, 24 Aug. 1992, *R. J. Bush s.n.* (MO-130269). **Kansas:** Geary Co., *F. C. Gates 18989* (MO); Riley Co., prairie W of Manhattan, *F. C. Gates 14967* (MO); prairie, *J. B. Norton 218* (MO). **Massachusetts:** Barnstable Co., sandy roadside, W Dennis, *M. L. Fernald 1078* (MO). **Michigan:** Midland Co., 4 mi. SE of Midland, *R. R. Dreisbach 6967* (PH). **Montana:** Cypress Hills, Battle Creek, Ranger Station, low prairie, *A. J. Breitung 5676* (MO); Sweetgrass Co., roadside, open grassland in foothills of Crazy Mtns. along Big Timber Creek, 6 Aug. 1945, *C. L. Hitchcock & C. V. Muhlick s.n.* (MO-1297352). **Nebraska:** Lancaster Co., Lincoln, Sep. 1898, *G. Hedgcock s.n.* (MO-130283); Scotts Bluff Co., 21 Aug. 1901, *C. F. Baker s.n.* (MO-130236); near bridge over a little creek outside Lincoln, *M. A. Wetter 305* (MO). **Nevada:** Washoe Co., Reno, *A. A. Heller 10639* (MO). **New Jersey:** Cape May Co., Dennisville, 10 Sep. 1916, *O. H. Brown s.n.* (PH). **Pennsylvania:** Westmoreland Co., New Alexandria, *F. W. Pennell 2581* (PH); Philadelphia Co., The Neck, 20 June 1912, *W. Findlay s.n.* (PH); Morris Arboretum, *J. M. Fogg Jr. 22274* (PH). **South Dakota:** Jackson Co., 6 mi. E of Belvidere, *G. J. Goodman 3290* (MO); Walworth Co., *S. S. Visher 3360* (MO). **Texas:** *J. Reverchon 471* (MO). **Utah:** Salt Lake Co., Parley Canyon, 7 mi. E from Salt Lake City, 23 Aug. 1931, *J. A. Moore & J. A. Steyermark s.n.* (MO-1027268). **Wisconsin:** Portage Co., Stockton, *W. R. Taylor 2802* (PH); Walworth Co., Tamarak Swamp, W of Lake Geneva, *J. A. Steyermark 65926* (MO). **Wyoming:** Albany Co., Laramie, *A. Nelson & E. Nelson 6894* (MO).

34a(2). Grindelia squarrosa f. **pseudopinnatifida** (D. Löve & J.-P. Bernard) Adr. Bartoli & Tortosa, comb. nov. *Grindelia perennis* A. Nelson f. *pseudopinnatifida* D. Löve & J.-P. Bernard, Svensk Bot. Tidskr. 53: 431. 1959. TYPE: Canada. Manitoba: Otterburne, roadside 1 mi. E of Otterburne, *J. P. Bernard 58/263* (holotype, MT digital image!; isotypes, DAO digital image!, MT digital image!).

Basal leaves pinnatisect. Chromosome number not known.

Distribution and habitat. *Grindelia squarrosa* f. *pseudopinnatifida* is documented only from Manitoba Province (Canada).

Phenology. *Grindelia squarrosa* f. *pseudopinnatifida* has been collected in August.

Etymology. The specific epithet is taken from the Greek for "pseudo," meaning "false," and the Latin "pinnatifidus," meaning "pinnately cleft," which refers to the pinnatisect leaves.

Discussion. This form was originally established for *Grindelia perennis* by Löve and Bernard in 1959. Pinnatisect basal leaves were only observed in the two specimens from Manitoba Province, Canada, while all specimens studied from the United States have basal leaves with entire margins.

Additional specimens examined. CANADA. **Manitoba:** Otterburne, *J. P. Bernard 58/510* (MT).

34b. Grindelia squarrosa var. **eligulata** (Steyerm.) Adr. Bartoli & Tortosa, comb. nov. Basionym: *Grindelia oxylepis* Greene var. *eligulata* Steyerm., Ann. Missouri Bot. Gard. 21: 490. 1934. *Grindelia eligulata* (Steyerm.) G. L. Nesom, Phytologia 68: 311. 1990. TYPE: Mexico. Coahuila: Saltillo, Sep. 1898, *E. Palmer 316* (holotype, GH [barcode] 00008454!; isotypes, MO-193822!, MO-193823!, NY [barcode] 169639!). Figure 15.

Heads discoid; involucre 8 mm broad. Achenes with longitudinal and transverse furrows. Chromosome number: $2n = 12$ (Powell & Turner, 1963: 135, sub *Grindelia oxylepis* var. *eligulata*; Pinkava & Keil, 1977: 681, sub *G. oxylepis* var. *eligulata*).

Distribution and habitat. *Grindelia squarrosa* var. *eligulata* grows in valleys with pines and junipers, from 1000 to 1900 m, in Coahuila and Nuevo León (Mexico).

Phenology. *Grindelia squarrosa* var. *eligulata* flowers from May to August.

Etymology. The name of the variety is taken from the Latin for "ligulatus," meaning "with ligule," and the prefix "e-," meaning "without or lacking," which refers to the absence of ligulate florets.

Discussion. *Grindelia squarrosa* var. *eligulata* has small discoid heads. It was considered a variety of *G. oxylepis* by Steyermark (1934), based on its achenes with furrows. However, *G. squarrosa* differs from *G. oxylepis* in the shape of the phyllaries, with a terete acumen in *G. squarrosa* and a subulate acumen in *G. oxylepis*.

Additional specimens examined. MEXICO. **Coahuila:** San Antonio, *J. Gregg 354* (MO); near Saltillo, 16 July 1848, *J. Gregg s.n.* (MO-130318); valley near Saltillo, *J. Gregg 97* (MO); 22 km NW of Fraile, in mtn. valley, *L. R. Stanford, K. L. Retherford & R. D. Northcraft 461* (MO); along Mexico 57, 0.1 mi. N of jct. of Mexico 57 & rd. to San Antonio, *C. C. Freeman & M. A. Wetter 2041* (NY); Sierra Zapaliname, *G. B. Hinton 20291* (MEXU). **Nuevo León:** along Mexico 57,

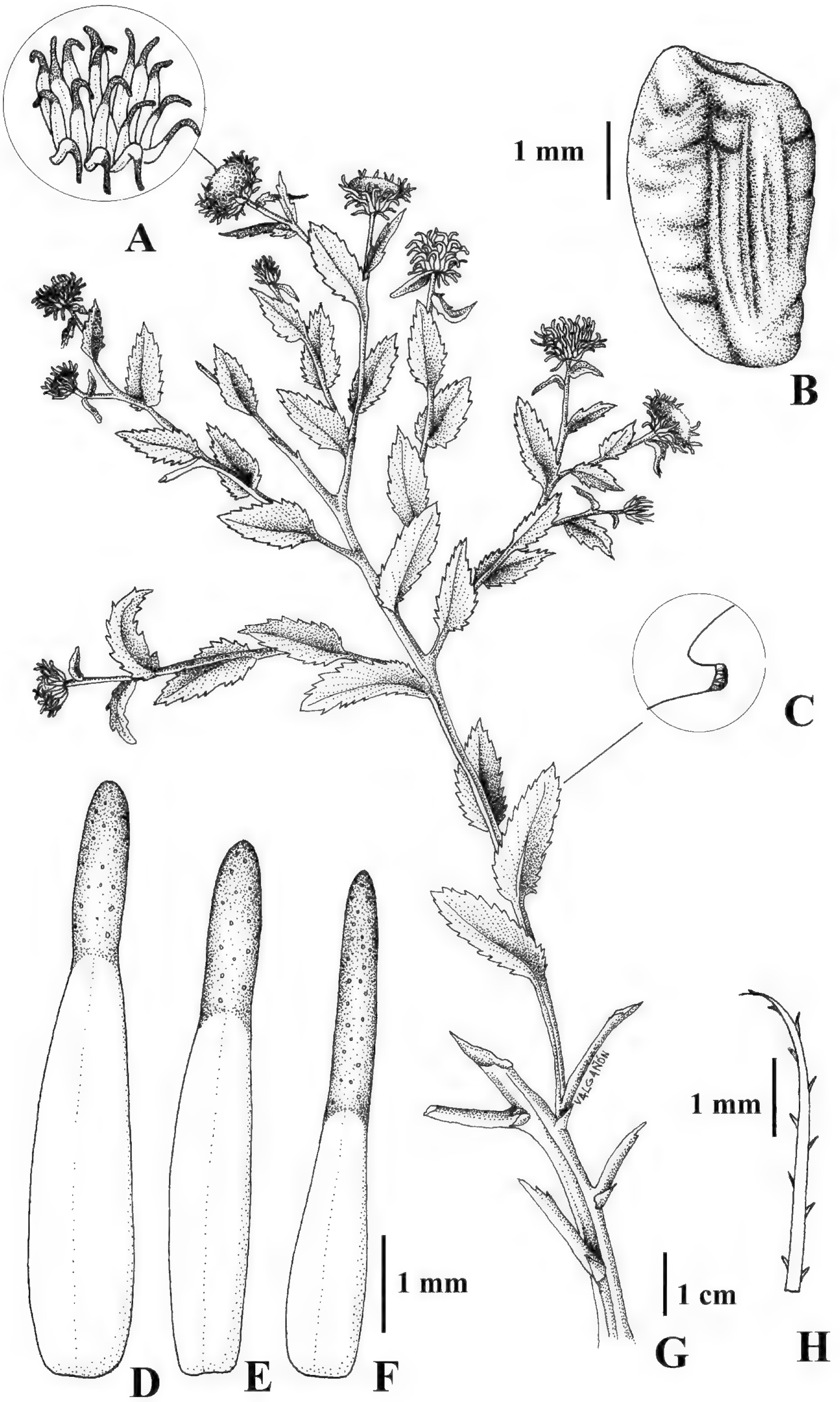

Figure 15. *Grindelia squarrosa* (Pursh) Dunal var. *eligulata* (Steyerm.) Adr. Bartoli & Tortosa. —A. Part of the involucre, inner phyllary series represented. —B. Achene, with furrows. —C. Leaf tooth, with rounded to obtuse apex, ending in a group of sessile glandular trichomes. D–F. Representative phyllaries. —D. Inner series. —E. Middle series. —F. Outer series. —G. Fertile habit. —H. Pappus, showing one of two setiform awns. Drawn from *E. Gregg 97* (MO).

6.4 mi. S of the Coahuila–Nuevo León state line, *C. C. Freeman & M. A. Wetter 2054* (NY); Mpio. Galeana, near Rancho Aguililla, *G. B. Hinton et al. 19581* (MEXU); N of Rancho Aguililla, *G. B. Hinton 27658* (MEXU).

34c. Grindelia squarrosa var. **nuda** (Alph. Wood) A. Gray, Syn. Fl. N. Amer. 1: 118. 1884. Basionym: *Grindelia nuda* Alph. Wood, Bot. Gaz. 3: 50. 1878. TYPE: U.S.A. Oklahoma: Indian Territory, s.d., *T. E. Wilcox s.n.* (holotype, NY [barcode] 00169629!; isotype, NY [barcode] 00169620!). Figure 16.

Grindelia aphanactis Rydb., Bull. Torrey Bot. Club. 31: 647. 1904, syn. nov. *Grindelia nuda* Alph. Wood var. *aphanactis* (Rydb.) G. L. Nesom, Phytologia 68: 323. 1990. TYPE: U.S.A. Colorado: Durango, on dry gravelly soil, 21 July 1898, *C. F. Baker, F. S. Earle & S. M. Tracy 526* (holotype, NY [barcode] 169594!; isotypes, F [barcode] 0050283F digital image!, MICH [barcode] 1107420 digital image!, MO-714083 digital image!, NY [barcode] 169595!, RM [barcode] 0001113 digital image!, RM [barcode] 0001114 digital image!).

Grindelia pinnatifida Wooton & Standl., Contr. U.S. Natl. Herb. 16: 178. 1913, syn. nov. TYPE: U.S.A. New Mexico: Rio Arriba Co., open slopes, vic. of Chama, 2380–2850 m, 9 July 1911, *P. C. Standley 6606* (holotype, US [barcode] 00127653 digital image!).

Grindelia squarrosa (Pursh) Dunal f. *angustior* Steyerm., Ann. Missouri Bot. Gard. 21: 481. 1934, syn. nov. [described under *Grindelia squarrosa* var. *nuda*]. TYPE: U.S.A. Texas: Floyd Co., in roadside marsh 16 mi. E of Lockney on Quitaque Rd., 23 Aug. 1921, *R. S. Ferris & C. D. Duncan 3391* (holotype, MO-902235!; isotypes, CAS [barcode] 7834 digital image!, GH [barcode] 00008441!, NY [barcode] 169629!).

Heads discoid; involucre 15–20 mm broad. Stems generally solitary. Achenes longitudinally furrowed. Chromosome number: $2n = 12$ (Raven et al., 1960: 126, sub *Grindelia aphanactis*; Pinkava & Keil, 1977: 681, sub *G. aphanactis*).

Distribution and habitat. *Grindelia squarrosa* var. *nuda* has been collected from rocky and sandy soils, in prairies and open forests, in Arizona, Colorado, Kansas, New Mexico, Oklahoma, and Texas (U.S.A). The variety has also been documented in pine and juniper forests, from 1200 to 1950 m, in Chihuahua and Coahuila (Mexico).

Phenology. *Grindelia squarrosa* var. *nuda* has been collected from May to October.

Etymology. The specific epithet is taken from the Latin "nudus," meaning "naked," which refers to the absence of ray florets.

Discussion. Nesom (1990) considered *Grindelia nuda* and *G. squarrosa* (the typical variety) as two different species, based on the shape of the achenes, a monomorphic form in *G. nuda* and dimorphic (those of the outer florets 3-angled and the inner, 4-angled) in *G. squarrosa*. This difference in the variety *nuda* of *G. squarrosa* is due to the absence of ray florets that give rise to the 3-angled achenes.

The type of *Grindelia aphanactis*, collected in the state of Colorado, matches the diagnostic characters of the typical *G. squarrosa* with the exception of the absence of ray florets, as in *G. squarrosa* var. *nuda*. It differs from the Mexican variety *eligulata* of *G. squarrosa* by the size of the heads.

In *Grindelia pinnatifida* the leaves are deeply toothed or pinnatisect, but the remaining characters correspond to those of the type of *G. squarrosa* var. *nuda*.

Additional specimens examined. MEXICO. **Chihuahua:** ca. 27 (air) mi. SSW of Columbus, *J. Henrickson 11213* (NY). **Coahuila:** Mpio. de Arteaga, Sierra Zapaliname, *R. Hilton et al. 20291* (GH). U.S.A. **Arizona:** Yavapai Co., roadside near Prescott, *J. A. Moore & J. A. Steyermark 3682* (MO). **Colorado:** Fremont Co., Coaldale, *J. A. Moore & J. A. Steyermark 3782* (MO); Montezuma Co., Cortez, *J. A. Moore & J. A. Steyermark 3775* (MO). **Kansas:** prairies, *A. Finch 6* (MO); Cullison Pratt Co., *M. W. Norris 197* (MO). **New Mexico:** Albuquerque Co., 19 Aug. 1883, *H. H. Rusby s.n.* (PH), *M. E. Jones 4140* (PH); San Miguel Co., Española, Santa Fe to Las Vegas, 7 Sep. 1881, *G. Engelmann s.n.* (MO-130063); 15 mi. NW of Las Vegas, *G. J. Goodman 2321* (MO); Union Co., along US 56/US 64, 3 km E of jct. with US 87 at Clayton Common but scattered in clay soil of ditch & adjacent pasture, *M. A. Wetter 502* (MO). **Oklahoma:** Comanche Co., dry open ground, granite areas, Wichita Mtns., Wichita Natl. Forest, *E. J. Palmer 41965* (MO); Greer Co., near Willow, *R. Stratton 332* (MO). **Texas:** Brown Co., dry open ground, Brownwood, *E. J. Palmer 11111* (MO); Childress Co., *Biology class 9014* (MO); Lipscomb Co., along Commission Creek, 3 mi. S of Higgins, forested area, *D. S. Correll 30251* (MO); Jeff Davis Co., Davis Mtns., along rd. to Toyahvale, 20 mi. from Ft. Davis, 10 June 1931, *J. A. Moore & J. A. Steyermark s.n.* (MO-1025879); Kendall Co., going W on Cascade, Caverns Rd., *M. A. Wetter 603* (MO); Llano Co., Enchanted Rock, *E. Whitehouse 9008* (MO); Potter Co., Amarillo, 1921, *M. Hebard s.n.* (PH).

35. Grindelia subalpina Greene, Pittonia 3: 297. 1898. TYPE: U.S.A. Wyoming: Laramie, 9 July 1896, *E. L. Greene s.n.* (holotype, NDG-53650 digital image!).

Grindelia platylepis Greene, Pittonia 3: 297. 1898. TYPE: U.S.A. Wyoming: Sherman, 29 July 1893, *E. L. Greene s.n.* (lectotype, designated here, NDG-53627 digital image!).

Grindelia erecta A. Nelson, Bull. Torrey Bot. Club 26: 356. 1899. *Grindelia subalpina* Greene var. *erecta* (A. Nelson) Steyerm., Ann. Missouri Bot. Gard. 21: 501. 1934. TYPE: U.S.A. Wyoming: Laramie Hills, 11 Sep. 1898, *A. Nelson 5306* (holotype, RM [barcode] 0001116 digital image!; isotypes, MO [barcode] 714074!, NY [barcode] 00169601!).

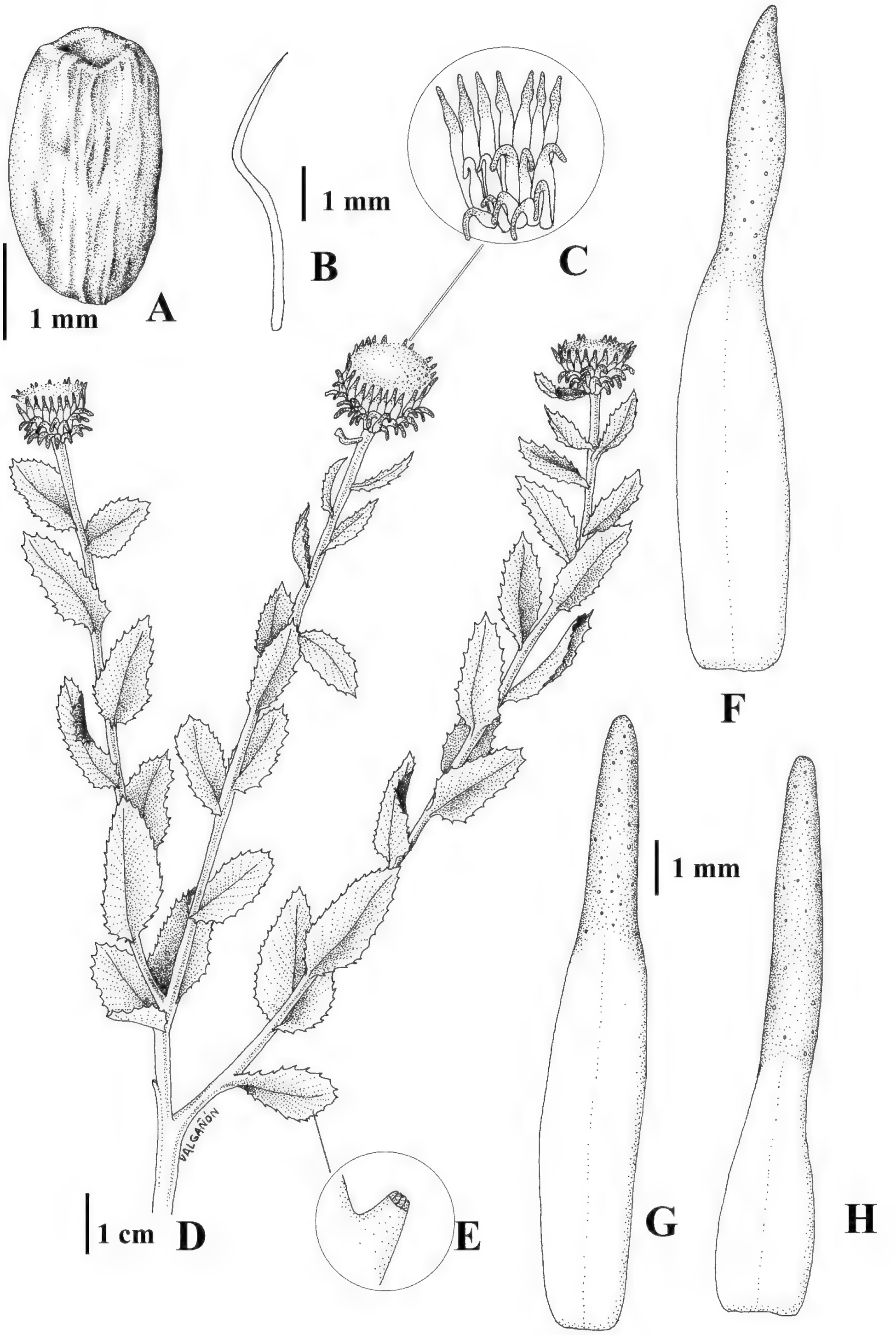

Figure 16. *Grindelia squarrosa* (Pursh) Dunal var. *nuda* (Alph. Wood) A. Gray. —A. Achene. —B. Pappus, showing one of two setiform awns. —C. Part of the involucre, inner phyllary series represented. —D. Fertile habit. —E. Leaf tooth, showing the rounded to obtuse apex, ending in a group of sessile glandular trichomes. F–H. Representative phyllaries. —F. Inner series. —G. Middle series. —H. Outer series. Drawn from *M. E. Jones 4140* (PH).

Grindelia acutifolia Steyerm., Ann. Missouri Bot. Gard. 21: 498. 1934, syn. nov. TYPE: U.S.A. New Mexico: Johnson's Mesa, 16 Aug. 1910, *E. O. Wooton s.n.* (holotype, US [barcode] 00127630!).

Perennial subshrubs, 0.15–0.6 m, with xylopodium; stems 1 to several, erect, ramified, glabrous. Leaves herbaceous, sessile, oblong to elliptic, 1.5–7 × 0.3–0.35 cm; blade apex acute or rounded, margin entire, minutely serrate or toothed, sometimes scabrous, teeth ending in a sclerotic tip, with sessile glandular trichomes on both surfaces; basal leaves with blades attenuate into a pseudopetiole; cauline leaves somewhat clasping. Heads radiate, pedunculate, 2.2–3.8 cm diam.; involucre broadly urceolate to hemispheric, resinous, 8–11 × 10–20 mm; phyllaries in 5 or 6 unequal series, graduated, acuminate, linear-oblong, 4–10 mm, erect; acumen terete, 2 mm long, reflexed or revolute, with sessile glandular trichomes. Ray florets 18 to 27; tube glabrous, ligule narrowly elliptic, 11–15 mm, apex entire. Disk florets with corolla 5–6 mm, with a gradually ampliate throat. Achenes light brown to stramineous, elliptic, 4-angled, 2.5–3 mm, smooth or slightly furrowed, truncate to weakly coronate; pappus of 2 to 8 setiform awns, 3.5–5.5 mm, straight, barbellulate. Chromosome number: $n = 6$ (Dunford, 1986: 302, sub *Grindelia acutifolia*).

Iconography. Steyermark (1934: 500, fig. 17).

Distribution and habitat. *Grindelia subalpina* has been collected in elevated planes, from 1600 to 2900 m, in Colorado, New Mexico, and Wyoming (U.S.A.).

Phenology. *Grindelia subalpina* flowers from July to August.

Etymology. The specific epithet is taken from the Latin "subalpinus," meaning "growing below the alpine region marked by the timber line."

Common name. Subalpine gumweed (<http://hortiplex.gardenweb.com>).

Discussion. Diagnostic characters for *Grindelia subalpina* include the reflexed or revolute, acuminate phyllaries, arranged in a graduated series, the flat phyllary acumen, and the leaves that have sessile glandular trichomes across both surfaces and not in pits. The species is similar to *G. havardii*, with which it shares basal leaves with blades attenuate into a pseudopetiole, the somewhat clasping cauline leaves, and the phyllaries of the involucre, which are acuminate and arranged in five or six graduated series. *Grindelia subalpina* differs by the teeth of the leaves that end in a sclerotic tip (vs. tipped by a group of sessile glandular trichomes in *G. havardii*) and the acumen of the phyllaries is flat (vs. terete or subterete in *G. havardii*). The pappus consists of two to four setiform awns in *G. subalpina* and two bristles in *G. havardii*.

We agree with Wetter who considered (1985, in sched.) that the Green specimen (NDG-53627) represents the type of *Grindelia platylepis*, and the name is lectotypified herein.

Grindelia acutifolia matches the diagnostic characters of *G. subalpina*. Steyermark (1934: 499) distinguished *G. subalpina* from *G. acutifolia* by the number of the pappus awns (four to eight in *G. subalpina* instead of two or three in *G. acutifolia*). However, in the protologue of *G. subalpina*, Greene (1898b: 297) stated "bristles of the pappus 2 to 4."

Additional specimens examined. U.S.A. **Colorado:** Boulder Co., meadows, near Middle St., Vrain Creek, 2 mi. W of Peaceful Valley P.O. near Raymond, *P. B. Green 274* (PH); Clear Creek Co., mtns. about the headwaters of Clear Creek, dry places in valley near Empire, *H. N. Patterson 235* (PH); El Paso Co., in Broadmoor Distr., Colorado Springs, *R. M. King & R. M. Garvey 12699* (MO); Fremont Co., *E. L. Johnston 335B* (MO); Gilpin Co., on approach to Rollins Pass, on railroad grade, 1.5 mi. from Moffat Tunnel Rd. W of Rollinsville, 30 Aug. 1986, *s. coll.* (MO-3440525); along Rollins Pass Rd., *R. Merrill King & R. M. Garvey 11914* (NY); Jefferson Co., pine jct., Woodcrest PK. access rd., *J. C. Semple & R. Brammall 2708* (MO); Park Co., along US Hwy. 285 ca. 1/2 mi. E of Bailey, *R. Merrill King & R. M. Garvey 12549* (MO). **New Mexico:** Albuquerque Co., *H. N. Rusby 1555* (NY); Colfax Co., along NM 72, 11.5 mi. W of jct. NM 72 & NM 325 at Folsom, *M. A. Wetter 908* (NY). **Wyoming:** Albany Co., Laramie, *A. Nelson & E. Nelson 6865* (MO); vacant lots, *G. J. Goodman 765* (MO); Laramie Co., near point where Tunnel Creek crosses Colorado, *D. Walter & B. Sears 9195* (MO); N city limits of Cheyenne, along Dell Range Blvd., N of Cheyenne Municipal Airport, *R. M. King & R. M. Garvey 12771* (MO); along old hwy. (Rd. 212-7) ca. 4 mi. E of Rd. 149-2, *R. M. King & R. M. Garvey 12781* (NY).

36. Grindelia subdecurrens DC., Prodr. (DC.) 5: 315. 1836. TYPE: Mexico. Guanajuato: Mpio. de Guanajuato, ca. Villapando, s.d., *Méndez s.n.* (holotype, G-DC, IDC microfiche!; isotype, GH [barcode] 00008458!).

Perennial subshrubs, 0.2–0.3 m; stems 2 to 5, erect, ramified, glabrous. Leaves subcoriaceous, sessile, ovate-oblong, 1.5–4 × 0.3–0.8 cm, clasping or cordate at the base; blade apex obtuse, margin minutely serrate to crenate, sometimes scabrous, teeth ending in a group of sessile glandular trichomes, with sessile glandular trichomes in pits on both surfaces. Heads radiate, pedunculate, 1.5–2 cm diam.; involucre hemispheric, resinous, 8–10 × 13–25 mm; phyllaries in 4 to 6 unequal series,

strongly graduated, acuminate, oblong-elliptic, 2.5–8 mm, spreading; acumen subterete, 1–4 mm, reflexed, with sessile glandular trichomes in pits, and sometimes with long simple hairs. Ray florets 20 to 30; tube glabrous, ligule elliptic, 5–11 mm, apex entire. Disk florets with corolla 4–5 mm, with an abruptly ampliate throat. Achenes dark brown, broadly elliptic to subquadrate, 3-angled or slightly compressed, 2–2.5 mm, with prominent longitudinal furrows, apex truncate; pappus of 2 to 4 bristles, 3–5 mm, straight, smooth. Chromosome number: $2n = 24$ (Semple et al., 1989: 302).

Iconography. Steyermark (1934: 468, fig. 10).

Distribution and habitat. *Grindelia subdecurrens* grows on pasturelands and in clearings of juniper forests, from 1900 to 2500 m, in Zacatecas, Aguascalientes, San Luis Potosí, and Guanajuato (Mexico).

Phenology. *Grindelia subdecurrens* flowers from late June to September.

Etymology. The specific epithet is taken from the Latin "sub-," meaning "somewhat" and "-decurrens," meaning "decurrent." It refers to the blade, which extends down along the stem.

Discussion. *Grindelia subdecurrens* is characterized by the radiate heads with acuminate phyllaries, arranged in strongly graduated series, with the acumen terete; its leaves show sessile glandular trichomes in pits on both surfaces. The taxon is similar to *G. camporum*, sharing ovate to oblong, clasping leaves with sessile glandular trichomes in pits on both blade surfaces, and with acuminate phyllaries of the involucre arranged in four to six unequal, graduated series. *Grindelia subdecurrens* differs by the size of plants (0.2–0.3 m vs. up to 1.5 m in *G. camporum*) and the heads (1.5–2 cm diameter vs. 2–3 cm diameter in *G. camporum*), and the teeth of the leaves that end in a group of sessile glandular trichomes (vs. in a sclerotic tip in *G. camporum*).

Additional specimens examined. MEXICO. **Aguascalientes:** Mpio. de Calvillo, Calvillo, *C. L. Díaz Luna 2533* (TEX); 18.9 km W of Ciudad Aguascalientes, turnoff to Gracias a Dios, *M. A. Lane 2689* (TEX); Hwy. 70 at turnoff to Gracias a Dios, ca. 10 mi. W of Aguascalientes, *A. T. Whittemore 82-016* (TEX). **Guanajuato:** Guanajuato, 5 km al ENE de Guanajuato, *R. Galván & J. D. Galván 3566* (XAL). **San Luis Potosí:** Mpio. de Charcas, 13.7 mi. N of Charcas, along a Tanque in pastureland, *J. Henrickson B6382* (TEX); Sierra de Monte Grande, *J. A. Reyes 267* (TEX). **Zacatecas:** 1 km E of turnoff to Station Frio from hwy. to Ciudad Durango to Ciudad Zacatecas, *M. A. Lane 2702* (TEX); 12 km of Jerez, 10 km SW of Malpaso, 29 June 1979, *R. Spellenberg et al. s.n.* (TEX [barcode] 00136682); betw. Fresnillo & Sombrerete along Hwy. 45, .6 mi. W of turnoff to Santa Rosa, *S. Sundberg 2911 with M. Lavin* (TEX); 14 mi. SW of Sombrerete, *U. T. Waterfall 13810* (TEX); stony mountainside 2.2 mi. SE of Sombrerete, *U. T. Waterfall 15578* (TEX).

37. Grindelia sublanuginosa Steyerm., Ann. Missouri Bot. Gard. 21: 458. 1934. TYPE: Mexico. Jalisco: S slopes of hills fronting Lake Chapala, 5 Jan. 1903, *E. W. Nelson 6523* (holotype, US [barcode] 00127661 digital image!; isotype, NY [barcode] 00169644!).

Perennial shrubs, 0.4–1.5 m; stems several, erect, ramified, with abundant long simple hairs and short stipitate glandular trichomes. Leaves herbaceous, sessile, oblong-elliptic, 2–4 × 0.5–1 cm, clasping; blade apex acute to acuminate, margin minutely serrate, teeth ending in a sclerotic tip or in few sessile glandular trichomes, with simple hairs and stipitate glandular trichomes on both surfaces, densely villous at the base. Heads radiate, sessile or subsessile, 1–1.5 cm diam.; involucre campanulate, resinous, 8–10 × 10–15 mm; phyllaries in 3 or 4 unequal series, graduated, acuminate, 7–9 mm, erect to spreading, the outer with stipitate glandular trichomes; acumen narrowly triangular. Ray florets 8 to 30; tube glabrous, ligule narrowly elliptic, 9–11 mm, apex entire. Disk florets with corolla 3.5–4.5 mm, with a gradually ampliate throat. Achenes dull brown, subquadrate, 3.5–4.5 mm, transverse and sometimes longitudinal furrows, apex truncate; pappus of 4 bristles, 3.5–4.5 mm, straight, smooth. Chromosome number not known.

Iconography. Steyermark (1934: 457, fig. 2).

Distribution and habitat. *Grindelia sublanuginosa* has been collected from rocky soil, from 1500 to 1600 m, at Lake Chapala in Jalisco (Mexico).

Phenology. *Grindelia sublanuginosa* has been collected in flower during January.

Etymology. The specific epithet is taken from the Latin "sub-," meaning "somewhat," and "lanuginosus," meaning "woolly," which refers to the hair-covering of the stems and leaves.

Discussion. In *Grindelia sublanuginosa*, the differentiating characters include the radiate, sessile or subsessile heads, the phyllaries in graduated series, with a phyllary acumen that is narrowly triangular, and the leaves bearing simple hairs and stipitate glandular trichomes on both surfaces, densely villous at the base.

Additional specimen examined. *Grindelia sublanuginosa* is known only from the type.

38. Grindelia tenella Steyerm., Ann. Missouri Bot. Gard. 21: 464. 1934. TYPE: Mexico. Tamaulipas: de Victoria a Tula, Nov. 1830, *J. L. Berlandier 766* (holotype, GH [barcode] 00008459!; isotypes, MO [barcode] 714073!, NY [barcode] 00169645!).

Annual herbs, 0.3–0.6 m; stems 1, sometimes 2, erect, ramified, glabrous or with dense simple hairs close to the head. Leaves herbaceous or subcoriaceous, oblong to obovate, 1.5–5 × 0.5–1.1 cm, clasping; blade apex acute or obtuse, margin denticulate or serrate-denticulate, teeth dull or ending in a sclerotic tip or in sessile glandular trichomes, with simple hairs and sessile glandular trichomes on both surfaces. Heads radiate, pedunculate, 2–2.5 cm diam.; involucre hemispheric, scarcely resinous, 6–8 × 9–13 mm; phyllaries in 4 or 5 unequal series, strongly graduated, acuminate, linear-elliptic, 3–4 mm, the outer bracts spreading and the middle bracts erect, with simple hairs; acumen subterete to terete, erect or somewhat curved, 1.5–2 mm, with scattered sessile glandular trichomes; the upper phyllaries narrowly elliptic, 8 mm, erect, with short acumen. Ray florets 15 to 18; tube glabrous, ligule narrowly elliptic, 7–9 mm, apex entire. Disk florets with corolla 4–5 mm, with an abruptly ampliate throat. Achenes dull brown, subquadrate, dimorphic, 2 mm, strongly furrowed to tuberculate, the innermost flattened with longitudinal superficial nerves, apex truncate; pappus of 2 or 3 bristles, 4–5 mm, straight, smooth. Chromosome number: $2n = 12$ (Zhao, 1996: 261).

Iconography. Steyermark (1934: 465, fig. 7).

Distribution and habitat. *Grindelia tenella* has been collected from grasslands with oak, and oak forests, from 200 to 1800 m, in Nuevo León and Tamaulipas (Mexico).

Phenology. *Grindelia tenella* has been collected in flower from June to late November.

Etymology. The specific epithet is taken from the Latin "tenellus," meaning "delicate," which refers to its slender habit.

Discussion. *Grindelia tenella* are annual herbs with radiate, pedunculate heads, with phyllaries having an acumen subterete to terete and arranged in graduated, four or five series; the achenes are strongly furrowed to tuberculate. The species is similar to *G. grandiflora* in that both are annual plants with sessile leaves, clasping, with sessile glandular trichomes on both blade surfaces, and have acuminate phyllaries arranged in graduated series. *Grindelia tenella* differs from *G. grandiflora* by the phyllary acumen that is subterete to terete (vs. filiform in *G. grandiflora*) and by the surface of the achenes (vs. striate or furrowed in *G. grandiflora*).

Additional specimens examined. MEXICO. **Nuevo León:** Mpio. Monterrey, Fundición, *Fr. G. Arsène & B. Abbon 101* (MO); El Cercado, *J. A. Duke 3974* (MO); Iturbide, Hwy. 31 to Los Tejotes, *G. B. Hinton et al. 28206* (MEXU). **Tamaulipas:** low grassland, Hacienda Santa Engracia, *V. H. Chase 7578* (MO); El Mirador, *G. B. Hinton et al. 24524* (MEXU, MO); rd. from Santa Engracia toward Dulces Nombres, 4.5 rd. mi. from lowermost crossing of Mimbres Creek, 12.5 rd. mi. NE of Paraje Los Caballos, *G. L. Nesom, M. Mayfield & J. Hinton 7452* (MO); on broad dry arroyo 19 km SE of Miquihuana on rd. to Palmillas, *L. R. Stanford, K. L. Retherford & R. D. Northcraft 867* (MO); 10 km NW of El Progresso, which is 18 km NW of Ocampo, *L. R. Stanford, K. L. Retherford & R. D. Northcraft 1084* (MO); 5 km S of Hoja Verde, in arroyo, *L. R. Stanford, L. A. Taylor & S. M. Lauber 2200* (MO).

39. Grindelia tricuspis (Sch. Bip.) Adr. Bartoli & Tortosa, comb. nov. Basionym: *Olivaea tricuspis* Sch. Bip., in Hooker's Ic. Pl. 12: 2–3, pl. 1103. 1876, non *Olivaea tricuspis* De Jong & Beaman, Brittonia 15: 89, fig. 1–9. 1963, nom. illeg. TYPE: Mexico. Jalisco: near Guadalajara, *W. Schaffner 346* (holotype, P not seen; isotype, fragm. at US [barcode] 00124577 digital image!).

Oligonema heterophylla S. Watson, Proc. Amer. Acad. Arts. 26: 138. 1891. *Golionema heterophyllum* (S. Watson) S. Watson, Bot. Gaz. 16: 267. 1891 [epithet ending corrected by S. Watson, 1891: 267, to neuter ending, cf. Art. 62.2c.]. TYPE: Mexico. México: Atlacomulco, in shallow water, del Río Hondo, 30 Aug. 1890, *C. G. Pringle 3236* (holotype, GH [barcode] 00010745 digital image!; isotypes, CAS [barcode] 0002852 digital image!, F [barcode] 0050822 digital image!, F [barcode] 0050823 digital image!, GH [barcode] 00010746 digital image!, GOET [barcode] 001582 digital image!, JE [barcode] 00000622 digital image!, K [barcode] 000221400 digital image!, M [barcode] 0030095 digital image!, MEXU-33259 digital image!, MO-3726402!, NY [barcode] 00230805 digital image!, RSA [barcode] 0001438 digital image!, TEX [barcode] 00373648 digital image!, US [barcode] 00127629 digital image!).

Aquatic rhizomatous herbs, 1–1.2 m; stems several, ramified, glabrous, fistulose. Leaves herbaceous, sessile; blade apex acute, with stipitate glandular trichomes when young; basal leaves sunken, lobed or pinnatisect, 4–10 × 0.5–1.5 cm; basal cauline leaves elliptic, 4–10 × 0.5–1.5 cm, margin entire or with 3 teeth near the apex, margin serrate, teeth ending in a sclerotic tip; upper leaves linear to elliptic, 1–3.5 cm, clasping, sometimes auriculate. Heads radiate, pedunculate, 3–4 cm diam.; involucre hemispheric, resinous, 10–15 × 15–20 mm; phyllaries in 3 or 4 subequal

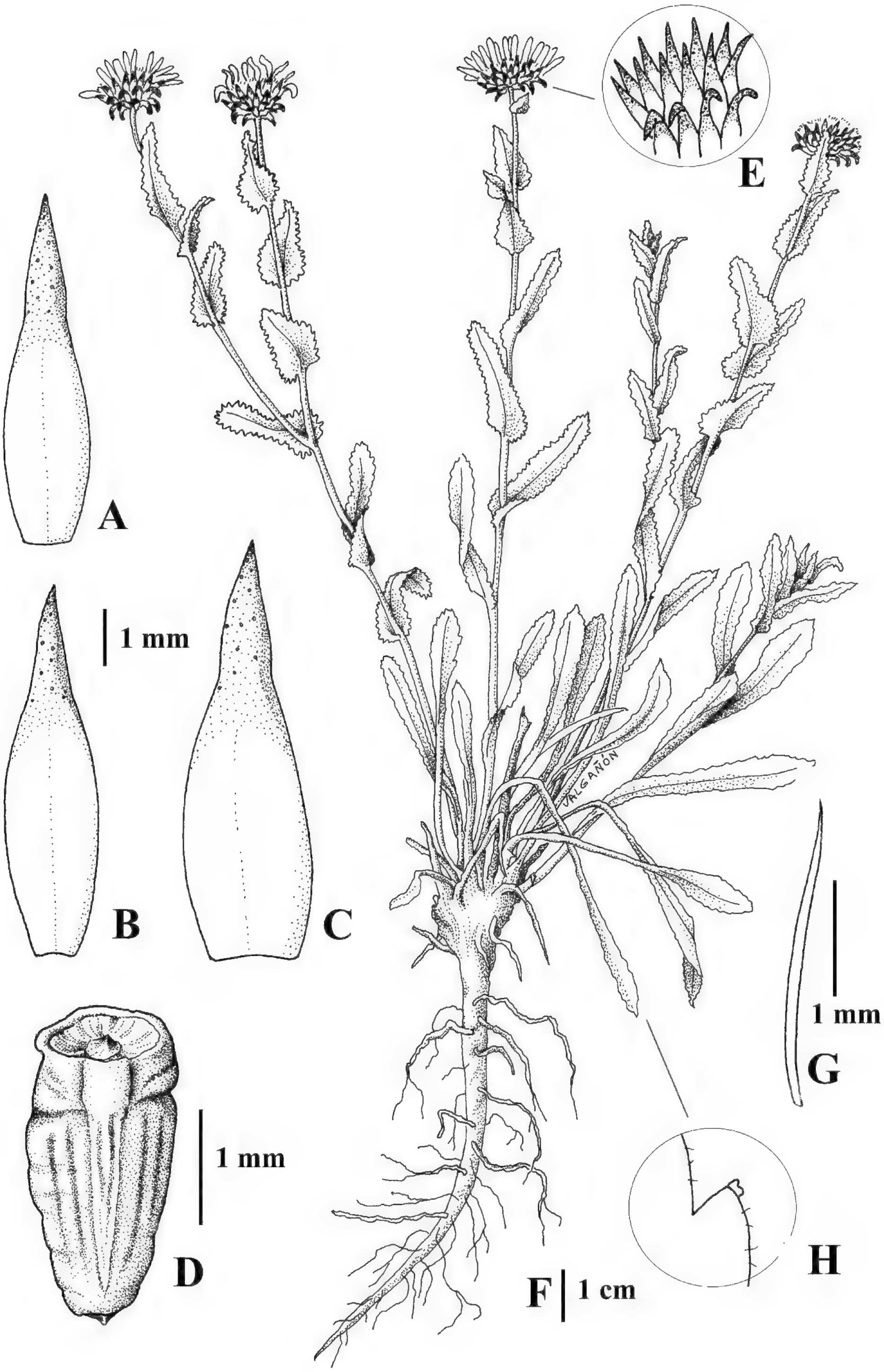

Figure 17. *Grindelia turneri* G. L. Nesom. A–C. Representative phyllaries. —A. Outer series. —B. Middle series. —C. Inner series. —D. Achene. —E. Part of the involucre; inner and middle phyllary series represented. —F. Fertile habit. —G. Pappus, one of two setiform awns. —H. Leaf tooth, ending in a group of sessile glandular trichomes. Drawn from *G. B. Hinton 17760* (TEX).

series, chartaceous and connate, narrowly triangular to narrowly ovate, 7–10 mm, subulate, erect, apex herbaceous, with stipitate glandular trichomes. Ray florets 25 to 35; tube with stipitate glandular trichomes, ligule linear-elliptic, 10–16 mm, apex entire or 3-toothed. Disk florets with corolla 4.5–5.5 mm, with an abruptly ampliate throat, tube with stipitate glandular trichomes. Achenes brownish green or light brown, quadrate, flattened, 2- or 3-winged, 2–3 mm, smooth, apex truncate; pappus of 5 to 12 bristles, 3–3.8 mm, barbellulate. Chromosome number: $n = 6$ (De Jong & Beaman, 1963: 90, sub *Olivaea tricuspis*).

Iconography. McVaugh (1984: 645, fig. 107), sub *Olivaea tricuspis*.

Distribution and habitat. *Grindelia tricuspis* grows on alkaline lowlands, from 1350 to 2040 m, in Aguascalientes, Jalisco, México, and Guanajuato (Mexico) (De Jong & Beaman, 1963).

Phenology. *Grindelia tricuspis* flowers from August to November.

Etymology. The specific epithet is taken from the Latin "tricuspis," meaning "ended in three cusps," which alludes to the apex of leaves.

Discussion. With its aquatic habit and fistulose stems, *Grindelia tricuspis* is similar to *G. leptocarpa*; both taxa are different from all other species in the genus (see Discussion under *G. leptocarpa*). In both species, the phyllaries are subulate and arranged in subequal series. These species differ in the basal leaves (sunken) that are lobed or pinnatisect in *G. tricuspis* (always entire in *G. leptocarpa*), the size of the heads (larger in *G. tricuspis* at 3–4 cm vs. 2–3 cm in *G. leptocarpa*) and the achenes that are 2- or 3-winged in *G. tricuspis* (vs. 2-angled in *G. leptocarpa*).

Beaman selected (in sched., 1963) the specimen GH-00010745 as holotype of *Oligonema heterophylla*, and his opinion is followed herein.

Additional specimens examined. MEXICO. **Aguascalientes:** El Llano, 1 km al NE de Palo Alto, *J. Martínez R. 1281* (INEGI). **Jalisco:** in flats above El Molino, ca. 25 mi. of Guadalajara, *R. McVaugh 16004* (NY); near Km. 57 just E of Aguascalientes state line, rd. from Ojuelos, *R. McVaugh 16934* (NY); Jalisco, hilly country, *O. Solbrig 4452* (NY); in shallow standing water at edge of Atotonilquillo, ca. 25 mi. SE of Guadalajara, *A. Cronquist 9811* (MEXU, NY); Mpio. Aradas, ca. 13.5 km S of Santa María del Valle, *R. McVaugh 26625* (NY).

40. Grindelia turneri G. L. Nesom, Phytologia 68: 313–314. 1990. TYPE: Mexico. Nuevo León: Mpio Galeana, betw. San Pablo & Tanquecillos, 0.5 mi. S of San Pablo, on rd. betw. San Rafael Jct. & Galeana, fallow fields in valley, pines on high slopes of valley margins, 2320 m, 27 Aug. 1989, *G. L. Nesom 7189 with J. Norris, J. Villarreal & M. Carranza* (holotype, TEX [barcode] 00373596!; isotypes, ANSM not seen, COLO [barcode] 368464 digital image!, ENCB not seen, F [barcode] 0050299F digital image!, GH [barcode] 00008461!, KANU [barcode] 305133 digital image!, MEXU-400620 digital image!, MO [barcode] 193881 digital image!, NY [barcode] 00169646!, US [barcode] 00289325 digital image!, WAT digital image!, WIS not seen). Figure 17.

Perennial subshrubs, 0.15–0.35 m, with xylopodium; stems several, prostrate with tips rising upward, not or few ramified, with scattered small simple hairs. Leaves herbaceous or subcoriaceous, sessile, oblong to oblong-elliptic, 1.5–4.5 × 0.4–0.9 cm, blade apex acute or obtuse, margin toothed, scabrous, teeth ending in a group of sessile glandular trichomes, with simple hairs or minutely stipitate glandular trichomes on both surfaces; basal leaves with blades attenuate into a pseudopetiole, blade apex obtuse; cauline leaves clasping; blade apex acute. Heads radiate, pedunculate, 1.4–2 cm diam.; involucre hemispheric-campanulate, resinous, 9–10 × 12–15 mm; phyllaries in 3 or 4 subequal series, acuminate, narrowly ovate, 7–10 mm, the outer and middle spreading, the upper erect; acumen subterete, triangular, 2–2.5 mm, erect or slightly reflexed, with sessile glandular trichomes. Ray florets 18 to 23; tube glabrous, ligule elliptic, 12–18 mm, apex entire. Disk florets with corolla 4.8–5.2 mm, with an abruptly ampliate throat. Achenes brown, elliptic, slightly flattened to 3-angled, 2–3 mm, smooth or with short, shallow, transverse incisions, barely tuberculate; pappus of 2 setiform awns, 5–5.5 mm, straight, smooth. Chromosome number not known.

Distribution and habitat. *Grindelia turneri* has been collected from silt soils, arid hills, and pine and yucca forests, from 970 to 2600 m, northwest of Galeana, in Nuevo León (Mexico).

Phenology. *Grindelia turneri* flowers from March to November.

Etymology. *Grindelia turneri* was named in honor of Billie Lee Turner (1925–), an American botanist at Texas University who worked extensively on the flora of Mexico.

Discussion. *Grindelia turneri* is characterized by its acuminate phyllaries, with the subterete, triangular phyllary acumen arranged in subequal, three or four series. Its leaves bear either simple hairs or minutely stipitate glandular trichomes on both blade surfaces,

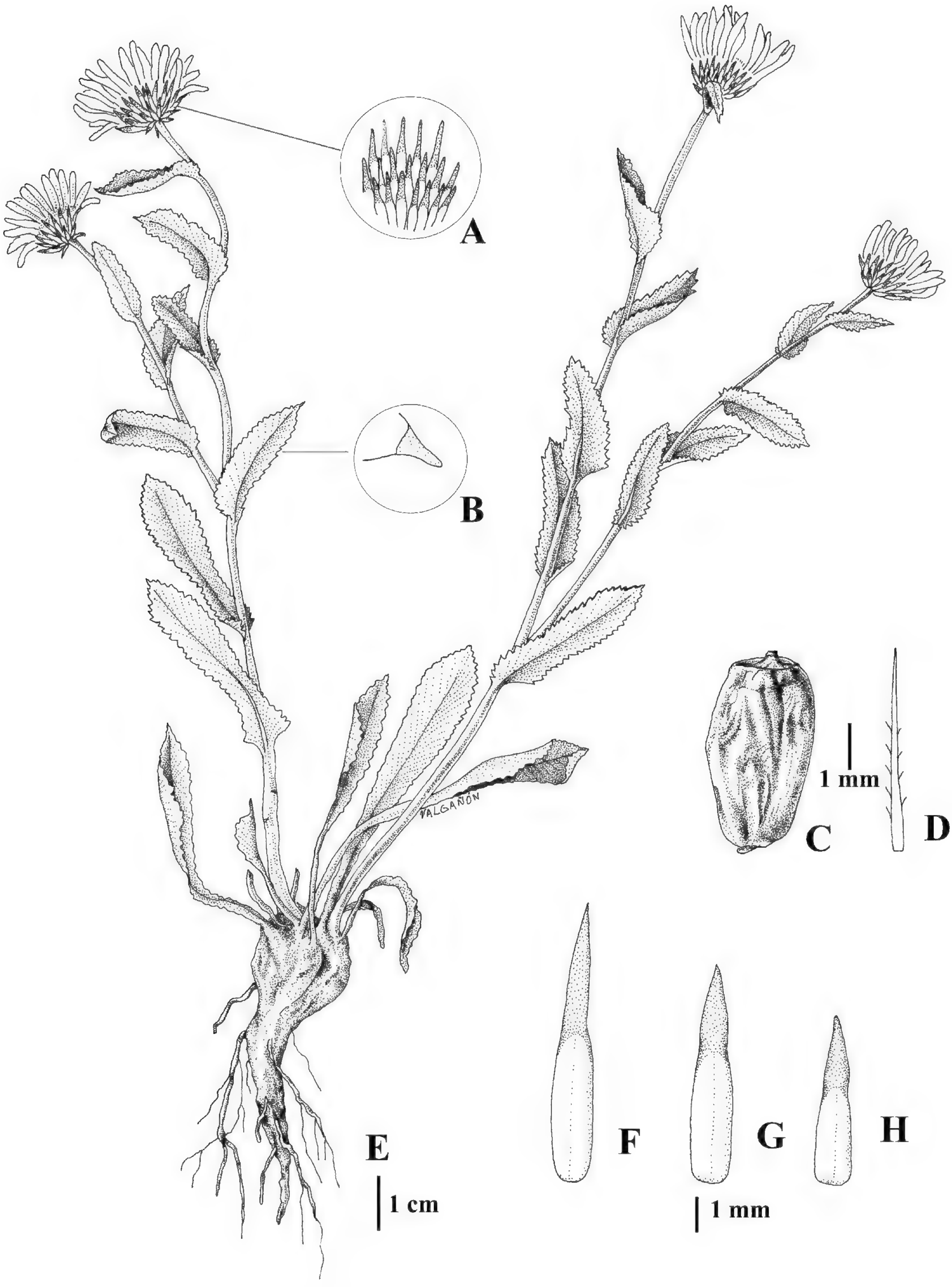

Figure 18. *Grindelia villarrealii* G. L. Nesom. —A. Part of the involucre, inner phyllary series represented. —B. Leaf tooth, showing the sclerotic apex. —C. Achene. —D. Pappus, one of two setiform, barbellate awns. —E. Fertile habit. F–H. Representative phyllaries. —F. Outer series. —G. Middle series. —H. Inner series. Drawn from *G. L. Nesom et al. 7149* (TEX).

and the marginal teeth are tipped by a group of glandular trichomes. *Grindelia turneri* is most closely related to *G. villarrealii*, both from the Mexican state of Nuevo León, sharing perennial duration with a xylopodium, basal leaves with attenuate blades into the pseudopetiole and the cauline leaves clasping, and a pappus of two setiform awns. *Grindelia turneri* differs by the leaves with teeth ending in a group of sessile glandular trichomes (vs. in a sclerotic tip in *G. villarrealii*), an involucre with phyllaries in subequal series (vs. unequal series), and smooth awns of the pappus (vs. barbellate).

Additional specimens examined. MEXICO. **Nuevo León:** Mpio. Aramberri, *G. B. Hinton 20518* (MEXU); Mpio. Galeana, Tanquecillos, *G. B. Hinton 17760* (MEXU, TEX); San Pablo to San Pedro Sotolar, *G. B. Hinton et al. 27192* (MEXU); Agua Blanca, *G. B. Hinton 22268* (TEX); a long gravel rd. 8.7 mi. E of the jct. of rd. & Mexico 57, *C. C. Freeman & M. A. Wetter 2056* (TEX); along rd. from San Rafael to Derecho de Marzo & Galeana, *J. Grimes et al. 2278* (TEX); 5.6 mi. ESE of San Pablo, E of San Rafael at jct. on hwy. 57, *G. L. Nesom 5281 with D. Morgan* (TEX); ca. 9 km S of San Rafael along Hwy. 57 to W San Roberto Jct. Broad Valley (Valle Potosí), W of town of San Pablo, on rd. from San Rafael jct. overlooking San Pablo, *G. L. Nesom et al. 7184* (TEX); 2 mi. S of Tanquecillos on rd. betw. San Rafael jct. & Galeana, *G. L. Nesom et al. 7192* (MO); 20.6 mi. N of San Roberto jct. along hwy. 57 to Saltillo, 50 m S of Km. 162 along E side of rd., *S. Sundberg 3131 with M. Lavin* (TEX); Socorro to San Pablo, *G. B. Hinton 25402* (MEXU); Rancho Aguililla, *G. B. Hinton 19481* (MEXU).

41. Grindelia villarrealii G. L. Nesom, Phytologia 73: 264–266. 1992. TYPE: Mexico. Nuevo León: Mpio. de Zaragoza, ca. 2–3 mi. N of Siberia on rd. to Zaragoza from San Antonio de Pena Nevada, broad valley, ca. 2500 m, area of oak & aspen at the bottom (N-facing margin) & agave-scrub on SW-facing slope, *Grindelia* around aspen grove, scattered but common at base of the slope in deep soil, 26 Aug. 1989, *G. L. Nesom 7149 with M. Carranza, J. Norris & J. Villarreal* (holotype, TEX [barcode] 00373597!; isotypes, ANSM not seen, MEXU-592176 digital image!). Figure 18.

Perennial subshrubs, 0.3–0.5 m, with xylopodium; stems 5 to 8, erect, ramified, glabrous or with scattered simple hairs. Leaves subcoriaceous to herbaceous, sessile; blade apex obtuse, margin serrate, teeth ending in a sclerotic tip, with dense sessile glandular trichomes on both surfaces, scarce simple hairs and minutely stipitate glandular trichomes; basal leaves obovate, 5–8 cm, attenuate into the pseudopetiole; cauline leaves, oblong-elliptic to oblong, 1.5–3 × 0.5–0.9 cm, clasping, somewhat auriculate, the uppermost sometimes acute at the apex. Heads radiate, pedunculate, 1.3–1.5 cm diam.; involucre hemispheric-campanulate, resinous, 6–10 × 10–15 mm; phyllaries in 3 or 4 unequal series, strongly graduated, subulate, linear-elliptic, 5–9 mm, spreading, apex flat, erect or reflexed. Ray florets 20 to 31; tube glabrous, ligule narrowly elliptic, 10–11 mm, apex entire. Disk florets with corolla 5–6 mm, with an abruptly ampliate throat. Achenes brown, elliptic, 4-angled, slightly flattened, 3–5 mm, slightly longitudinally rugose, barely tuberculate, apex truncate; pappus of 2 setiform awns, 4–5 mm, barbellate. Chromosome number not known.

Distribution and habitat. *Grindelia villarrealii* has been collected from areas with oak, poplar, and *Agave* L., at ca. 2500 m, in Nuevo León (Mexico).

Phenology. *Grindelia villarrealii* has been collected in August.

Etymology. *Grindelia villarrealii* was named in honor of José Ángel Villarreal Quintanilla (1956–), curator of ANSM.

Discussion. *Grindelia villarrealii* is known only through the type collection. Its heads are small, no more than 1.5 cm in diameter, and radiate, with subulate phyllaries in strongly graduated, three or four series. The marginal teeth of the leaves end in a sclerotic tip, and both blade surfaces present dense, sessile glandular trichomes, with scattered simple hairs and minute, stipitate glandular trichomes. The taxon is close to the sympatric species *G. turneri* but differs by the marginal teeth of the leaves, the phyllaries, and the pappus awns (see Discussion under *G. turneri* above).

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Appendix 1. Index to collectors. Each specimen is cited by the last name of the first collector when there is more than one collector. The species number in parentheses refers to the number of the species in the text and the List of Species below.

List of Species

1. *Grindelia adenodonta* (Steyerm.) G. L. Nesom
2. *Grindelia arizonica* A. Gray
3. *Grindelia camporum* Greene
4. *Grindelia confusa* Steyerm.
5. *Grindelia decumbens* Greene
6. *Grindelia fastigiata* Greene
6a. *Grindelia fastigiata* Greene var. *fastigiata*
6b. *Grindelia fastigiata* Greene var. *revoluta* (Steyerm.) Adr. Bartoli & Tortosa
7. *Grindelia fraxinipratensis* Reveal & Beatley
8. *Grindelia grandiflora* Hook.
9. *Grindelia greenmanii* Steyerm.
10. *Grindelia hallii* Steyerm.
11. *Grindelia havardii* Steyerm.
12. *Grindelia hintoniorum* G. L. Nesom
13. *Grindelia hirsutula* Hook. & Arn.
14. *Grindelia hirtella* (B. L. Rob. & Greenm.) Adr. Bartoli & Tortosa
15. *Grindelia humilis* Hook. & Arn.
15a. *Grindelia humilis* Hook. & Arn. var. *humilis*
15b. *Grindelia humilis* Hook. & Arn. var. *platyphylla* (Greene) Adr. Bartoli & Tortosa
16. *Grindelia integrifolia* DC.
16a. *Grindelia integrifolia* DC. f. *integrifolia*
16b. *Grindelia integrifolia* DC. f. *dentata* Steyerm.
17. *Grindelia inuloides* Willd.
17a. *Grindelia inuloides* Willd. var. *inuloides*
17b. *Grindelia inuloides* Willd. var. *glandulosa* (Greenm.) Steyerm.
17c. *Grindelia inuloides* Willd. var. *latamplexa* G. L. Nesom
18. *Grindelia laciniata* Rydb.
19. *Grindelia lanceolata* Nutt.
19a. *Grindelia lanceolata* Nutt. var. *lanceolata*
19b. *Grindelia lanceolata* Nutt. var. *greenei* (Steyerm.) G. L. Nesom
19c. *Grindelia lanceolata* Nutt. var. *subincisa* (Greene) Adr. Bartoli & Tortosa
19d. *Grindelia lanceolata* Nutt. var. *texana* (Scheele) Shinners
20. *Grindelia leptocarpa* (De Jong & Beaman) Adr. Bartoli & Tortosa
21. *Grindelia macvaughii* G. L. Nesom
22. *Grindelia microcephala* DC.
23. *Grindelia nana* Nutt.
23a. *Grindelia nana* Nutt. var. *nana*
23b. *Grindelia nana* Nutt. var. *columbiana* Piper
24. *Grindelia nelsonii* Steyerm.
25. *Grindelia oaxacana* G. L. Nesom
26. *Grindelia obovatifolia* S. F. Blake
27. *Grindelia oolepis* S. F. Blake
28. *Grindelia oxylepis* Greene
29. *Grindelia palmeri* Steyerm.
30. *Grindelia paysonorum* H. St. John
31. *Grindelia pusilla* (Steyerm.) G. L. Nesom
32. *Grindelia robinsonii* Steyerm.
33. *Grindelia scabra* Greene
34. *Grindelia squarrosa* (Pursh) Dunal
34a. *Grindelia squarrosa* (Pursh) Dunal var. *squarrosa*
34a(1). *Grindelia squarrosa* (Pursh) Dunal f. *squarrosa*
34a(2). *Grindelia squarrosa* (Pursh) Dunal f. *pseudopinnatifida* (D. Löve & J.-P. Bernard) Adr. Bartoli & Tortosa
34b. *Grindelia squarrosa* (Pursh) Dunal var. *eligulata* (Steyerm.) Adr. Bartoli & Tortosa
34c. *Grindelia squarrosa* (Pursh) Dunal var. *nuda* (Alph. Wood) A. Gray
35. *Grindelia subalpina* Greene
36. *Grindelia subdecurrens* DC.
37. *Grindelia sublanuginosa* Steyerm.
38. *Grindelia tenella* Steyerm.
39. *Grindelia tricuspis* (Sch. Bip.) Adr. Bartoli & Tortosa
40. *Grindelia turneri* G. L. Nesom
41. *Grindelia villarrealii* G. L. Nesom

Abrams L. 3957 (10); Alexander A. M. 3712 (15a); Ammerman E. s.n. (22); Anderson G. R. s.n. (15a); Arredondo D. G. 227 (28); Arsène Fr. G. 101 (38).

Baird C. 1397 (23b); Baker C. F. 497 (5), 538 (2), 526 (34c), 682 (2), 683 (19c), 1701 (3), s.n. (34a1); Barriga H. D.

2492 (17a); Bartram E. B. s.n. (15a); Beatley J. s.n. (7), s.n. (7); Berlandier J. L. 766 (38); 2057 (22); Bernard J. P. 58/263 (34a2), 58/510 (34a2); Bioletti F. T. s.n. (3); Biology class 9014 (34c); Blankinship J. W. s.n. (23a); Blumer J. C. 4 (33); Bolander H. N. 389 (13), 6493 (15b); Botany Beechey's Voyage s.n. (13), s.n. (15); Bradley A. 477 (16a); Brandegee K. s.n. (15b); Breedlove D. E. 59348 (29), 63552 (9); Breitung A. J. 5676 (34a1); Bremer K. 2325 (31); Brewer W. H. 850 (3); Brown H. E. 599 (23a); Brown O. H. s.n. (34a1); Brunsfeld S. J. 79438 (30); Burch D. 5139 (29); Burtt Davy J. 1383 (15a), s.n. (15a); Bush B. F. 220 (19a); Bush R. J. s.n. (34a1).

Candolle A. de s.n. (16); Canne-Hilliker J. M. 1941 (17c); Carter J. L. 1961 (34a1); Chandler H. P. 5460 (10); Chas C. D. 36 (34a1); Chase V. H. 7266 (32), 7376 1/2 (32), 7578 (38); Chiang F. 9170 (19d); Chittenden E. M. 104 (9); Christ J. H. 11478 (23a); Clemens J. 948 (1); Clokey I. W. 4323 (6a), 4324 (6a); Collom R. E. 463 (2); Colwell A. 85 (16a); Congdon J. W. s.n. (15a); Correll D. S. 20165 (4), 30251 (34c); Cory V. L. 5013 (8), 40706 (8), 50544 (8), 51421 (27), 52450 (8); Cotton J. S. 780 (23b); Cowen J. M. s.n. (34a1); Craig C. F. 1774 (6b); Cronquist A. 9759 (29), 9811 (39).

Demaree D. 9235a (15b), 10248 (3), 10424 (13), 10469 (3), 10522a (3), 10523 (13), 13192 (19d); Davidson A. 736 (2); De Jong D. C. D. 971 (20); Díaz Luna C. L. 2533 (36), 13168 (17a); Diwart F. M. s.n. (19a); Douglas D. 55 (13); Dreisbach R. R. 6967 (34a1); Drushel J. A. s.n. (6a); Duke J. A. 3974 (38); Dunford M. P. 1156 (27), 1157 (8), 1173 (6a).

Earle F. S. 509 (11); Eastwood A. 63 (6a), 280 (13), 794 (15b), s.n. (13); Edwin B P. 1883 (30); Eggert H. s.n. (8); Elmer A. D. E 4267 (13); Encina J. A. 821 (8), 826 (8); Engelmann G. 650 (34a1), s.n. (34c); Ertter B. 10142 (13); Escobedo J. M. 2509 (17a); Eyerdam W. J. 1150 (15a), 1179 (15a), 1302 (15a), s.n. (15a), s.n. (15a).

Fernald M. L. 1078 (34a1); Fernández R. 4834 (17a); Ferris R. S. 3391 (34c); Finch A. 6 (34c); Findlay W. s.n. (34a1); Fisher L. 37145 (32), 44165 (28); Fogg J. M. Jr. 22274 (34a1); Franklin B. 4350 (6a); Freeman C. C. 2041 (34b), 2054 (34b), 2056 (40), 2137 (33); Friberg G. N. s.n. (15a).

Galván R. 3566 (36); Garza F. 4265 (9); Gates F. C. 14967 (34a1), 18989 (34a1); Ginzbarg S. 180 (9); González-Martínez 102 (14); Goodman G. J. 765 (35), 2321 (34c), 3290 (34a1); Gorman s.n. (15a); Grant J. M. s.n. (15a); Green P. B. 274 (35); Greene E. L. 974 (23a), s.n. (3), s.n. (5), s.n. (6), s.n. (6a), s.n. (13), s.n. (15a), s.n. (15a), s.n. (15a), s.n. (15b), s.n. (35), s.n. (35); Gregg J. 97 (34b), 354 (34b), 444 (28), 627 (28), s.n. (34b); Grimes J. 2278 (40); Guevara E. s.n. (4); Gutiérrez R. s.n. (17a); Gutierrez S. 1 (17a); Guzmán R. 953 (17a).

Haenke T. s.n. (15a); Hall E. 266 (16a); Hansen G. 172 (15a), 1672 (15a); Harford W. G. W. s.n. (15a); Harrison G. J. 8334 (2); Hasse H. E. s.n. (3); Hebard M. 2156A (5), s.n. (34c); Hedgcock G. s.n. (34a1); Heller A. A. 1820 (1), 1840 (15a), 3418 (23a), 5578 (15a), 5810 (15a), 7461 (13), 7542 (15a), 8117 (15a), 8575 (13), 10639 (34a1), 10780 (15a), 12979 (23a), 13764 (15a), 15483 (3), 16312 (3), s.n. (15a); Henderson L. F. 432 (16a), 433 (15a), 434 (16a), 435 (23b), 1676 (15a), 2791 (30), 13987 (15a), s.n. (16a); Henrickson J. 5802a (28), 5988 (28), B6382 (36), 11213 (34c); Henry J. K. s.n. (15a), s.n. (15a), s.n. (15a); Hilton R. 20291 (34c); Hinton G. B. 2131 (26), 11919 (17a), 17760 (40), 18344 (9), 18618 (26), 18666 (12), 19481(40), 19581 (34b), 19831 (9), 19865 (9), 20024 (26), 20205 (9), 20291 (34b), 20398 (17a), 20518 (40), 20996 (9), 21161 (26), 21316 (26), 21434 (26), 22268 (40), 22398 (26), 22434 (9), 24382 (9), 24524 (38), 25335 (9), 25388 (9), 25402 (40), 25428 (9), 27192 (40), 27658 (34b), 28206 (38); Hitchcock C. L. s.n. (34a1); Hoffmann R. s.n. (3); Howe M. A. s.n. (15b); Howell J. T. 2786 (3), 4304 (13), 4352 (13), 4550 (3), 5201 (15a), 5221 (13), 5223 (13), 5329 (3), 5338 (13), 5346 (15a), 5473 (15b), 5496 (3), 5550 (3), 6566 (3), 7545 (15a), 8106 (15b), 8133 (3), 10796 (15a), 10805 (15a), 10827 (3), 10842 (3), 10849 (3), 10861 (15b), 11394 (13), 11414 (13), 11415 (13), 11436 (13), 11455 (13), 11456 (13), 11457 (13), 11462 (3), 11463 (13), 11648 (3), 11658 (15b), 11692(3), 11710 (15a), 11721 (3), 11723 (15a), 21491 (13), s.n. (16a); Humboldt F. W. s.n. (17a).

Isle D. 478 (15a).

Jackson R. C. 5097 (28); Johnston E. L. 335B (35); Johnston I. M. 8881 (11); Jones G. N. 3442 (15a), s.n. (15a), s.n. (15a); Jones M. E. 4140 (34c), s.n. (13); Jones N. 354 (23b); Jones Q. 277 (30); Joor J. F. s.n. (19a); Jowel J. 6574 (3).

Keck D. D. 2943 (15b); Kellogg A. s.n. (13); Kenoyer J. M. 2778 (17b), s.n. (19b); King R. M. 2631 (25), 12699 (35), 12771 (35), Kral R. 27380 (28), 44003 (19a).

Lane M. A. 2273 (4), 2276 (4), 2594 (21), 2689 (36), 2702 (36), 3088 (10), 3093 (3), 3097 (3), 3098 (3), 3138 (15a); Lebgue T. 3316 (4); Lesica P. 5789 (30); LeSueur D. H. 974 (28), 1016 (4); Lewis M. 40 (34); Lindheimer F. 255 (1), 418 (19d), 919 (1); Lodewyks M. C. 80 (19a); Loockerman D. J. 40015 (29); Lundell C. L. 18644 (19d); Lunell J. 1040 (34a1); Lusk S. D. s.n. (31); Lyall D. s.n. (15a).

Macoun J. 420 (15a), 421 (16a), s.n. (15a); Mahler W. F. 8653 (27); Marcus E. 29142 (15a), s.n. (22); Martínez R. J. 1281 (39); McKechnie B. E. 283 (11); McVaugh R. 12820 (21), 16004 (39), 16934 (39), 26625 (39); Méndez s.n. (36); Merrill King R. 2631 (25), 2934 (17b), 11914 (35), 12549 (35), 12781 (35); Metcalfe O. B. 744 (2), 1302 (33); Metz M. C. s.n. (22); Meyer F. G. 1588 (15a), 2988 (9); Moore J. A. 3004 (22), 3043 (33), 3151 (11), 3183 (6a), 3607 (11), 3682 (34c), 3683 (3), 3684 (15a), 3685 (15b), 3686 (15a), 3687 (15b), 3688 (23a), 3768 (34a1), 3770 (6a), 3771 (6a), 3773 (2), 3775 (34c), 3778 (5), 3780 (5), 3781 (34a1), 3782 (34c), 3784 (6b), 3785 (6b); Moore J. A. s.n. (23a), s.n. (34a1), s.n. (34c); Mueller C. H. 896 (17a), 2173 (9), 2932 (26); Munz P. A. 11157 (3), 12916 (3), 17997 (10).

Neff J. L. 8-19-91-3 (2); Nelson A. 4988 (34a1), 5306 (35), 6865 (35), 6894 (34a1); Nelson E. W. 6523 (37), 6864 (24); Nelson J. C. 1670 (16b); Nesom G. L. 4800 (9), 5281 (40), 6660 (28), 6789 (26), 7086 (26), 7105 (17b), 7149 (41), 7184 (40), 7189 (40), 7192 (40), 7194 (17b), 7198 (9), 7452 (38), 7587 (12), 7718 (26); Norris M. W. 197 (34c); Norton J. B. 218 (34a1); Nuttall T. s.n. (15a), s.n. (16a), s.n. (16a), s.n. (17a), s.n. (23), s.n. (23a), s.n. (23b).

Orcutt C. R. 1204 (19b), s.n. (10), s.n. (10); Oswald V. 4408 (3), 4410 (3); Ownbey M. 1403 (5).

Palmer E. 128 (10), 163 (29), 174 (28), 248 (15b), 316 (34b), 469 (31), 471 (9), 472 (8), 520 (28); Palmer E. J. 4161 (19a), 10134 (1), 10249 (19d), 11111 (34c), 11295 (31), 12855 (19d), 29364 (19a), 31465 (19a), 33055 (19a), 33590 (1), 37831 (23a), 41965 (34c), 42014 (19d); Parish S. B. 4452 (3); Parks H. E. O. 411 (15a), 24190 (15b); Parry C. C. 371 (29), s.n. (8); Patterson H. N. 235 (35); Peck M. E. 13359 (15a); Peirson F. W. 4825 (10), 8190 (3); Pennell F. W. 2581 (34a1), 5478 (19d), 17006 (12), 24683 (6b); Pérez E. 1632 (17a); Pierce J. R. 1120 (30), 1146 (30); Pilsbry H. A. s.n. (33), s.n. (33); Pitcher Z. s.n. (19); Powell A. M. 585 (17a), 616 (17a), 714b (17b); Pringle C. G. 748 (28), 3236 (39), 4805 (14), 6962 (17b), 9913 (17b); Purer E. A. 4994 (3), 5045 (3), 5462 (3), 5902 (3); Purpus C. A. 2466 (17b), 2514 (14), 4701 (28), 5151 (32), 5722 (32).

Redfearn P. L. Jr. 33149 (19a); Redfield J. H. 2964 (6a); Reeves T. P 13009 (8); Reveal J. L. 1536 (7), 1887 (7), 2107

(7); Reverchon J. 471 (34a1); Reyes J. A. 267 (36); Rigg G. B. s.n. (15a); R. M. A. 725 (15a); Roadhouse J. E. 65 (13); Rodríguez A. 1292 (17a); Rodriguez J. D. s.n. (17a); Roe K. 144 (29); Rollins R. C. 2691 (15a); Rose L. S. 33221 (13), 33315 (15a), 33348a (3), 33367 (15a), 40364 (15a); Rothrock J. T. 796 (2); Runyon R. 506 (27), s.n. (27); Rusby H. H. 206 (2), 1555 (35), s.n. (34c); Ruth A. 64 (8), 284 (1); Rydberg P. A. 9210 (18), 9692 (18).

S. coll. (35); Sandberg, J. H. 784 (23a); Sanders R. W. 1067 (17a); Savage T. E. s.n. (23a); Schaffner J. G. 738 (28); Schaffner W. 346 (39); Schmidt H. H. 864 (15a); Schmitt W. F. s.n. (15b); Semple J. C. 2708 (35); Setchell W. A. s.n. (15b); Shantz H. L. 597 (6a); Sheldon E. P. 10960 (23b); Smith C. L. 686 (14); Smith C. P. 1016 (15b); Smith L. C. 135 (25); Solbrig O. 4452 (39); Spalding R. s.n. (23a); Spellenberg R. 4042 (28), s.n. (36); Standley P. C. 6606 (34c); Stanford E. E. 719 (3), 969 (15a); Stanford L. R. 461 (34b), 867 (38), 1084 (38), 2200 (38); St. John H. 4361 (30); Stephenson M. R. 126 (19d); Stewart R. M. 1702 (19d); Steyermark J. A. 24602 (19a), 65926 (34a1); Stittler C. I. s.n. (19d); Stratton R. 332 (34c); Suksdorf W. N. 8 (3), 279 (13), s.n. (23b); Sundberg S. 1890 (26), 2911 (36), 3131 (40).

Taylor M. 24 (12); Taylor M. S. 4256 (23a), 5189 (15b); Taylor T. M. C. 3009 (15a); Taylor W. R. 2802 (34a1); Tenorio Lezama P. 6733 (17b), 20201 (25); Tharp B. C. 44451 (27); Thomas R. D. 20565 (19a), 20964 (19a); Thompson J. W. 4745 (23a), 4945 (23a), 7164 (23b), 7855 (15a), 9959 (15a), 10091 (15a), 11119 (23b), 17376 (23a); Tracy J. P. 4669 (23a); Trelease W. s.n. (19a); Turner B. L. 76-13 (17c), 15329 (17a).

Umbach L. M. s.n. (23b).

Van der Werff H. 6058 (10), 8707 (10); Ventura P. 15435 (17a); Villarreal J. A. 2312 (28), 2351 (26); Visher S. S. 3360 (34a1).

Walker H. A. 430 (15a); Walter D. 9195 (35), 10549(2), 10742 (5), 11546 (6b); Walter R. G. 4644 (5); Waterfall U. T. 13810 (36), 13869 (21), 15578 (36), 15641 (17a); Weber W. A. 2232 (23a); Welsh S. L. 12631 (6a); Wetter M. A. 77 (18), 305 (34a1), 483 (19a), 485 (19), 502 (34c), 568 (6a), 590 (33), 603 (34c), 605 (1), 700 (2), 720 (18), 729 (6b), 737 (27), 738 (27), 774 (2), 822 (6a), 836 (6a), 888 (18), 908 (35), 920 (6b), 925 (6b), 955 (2), 956 (19c), 961 (19c), 964 (19c), 969 (2), 1008 (19d), 1010 (19d), 1012 (8), 1031 (19c), 1033 (2), 2035 (27); Whitehouse E. 9008 (34c), 16425 (1); Whittemore A. T. 82-016 (36); Wilcox T. E. s.n. (34c); Wilder P. 4375 (15b); Wilkes Expedition s.n. (15a); Williamson C. S. s.n. (15a); Wolf C. B. 8101 (3), 8619 (15a); Wooton E. O. 224 (33), 372 (33), 2568 (2), s.n. (33), s.n. (35); Worthington R. D. 8963 (20); Wright s.n. (8).

Zamudio S. 2336 (17a), 2663 (17a); Zeller S. M. 956 (15a), s.n. (15a).

SYSTEMATICS OF *PATERSONIA* (IRIDACEAE, PATERSONIOIDEAE) IN THE MALESIAN ARCHIPELAGO[1]

Peter Goldblatt[2]

ABSTRACT

The predominantly Australasian genus *Patersonia* R. Br. (Iridaceae, Patersonioideae) includes 18 species in Australia, one in New Caledonia, and just one currently recognized species in the Malesian archipelago, although two more have been described previously but are now reduced to synonymy. After examining the available collections of the genus from this vast area, I have identified two distinct sets of populations in Borneo, two more in New Guinea, one in Sumatra, and one in Mindoro, The Philippines. Many collections lack flowers or are poorly preserved, yet greater-than-expected differences in vegetative and some fruit features for a single species are evident among the six population sets. Morphological variation includes leaf size; marginal vestiture and microscopic surface structure; flowering stem orientation, width, and length relative to leaves; inflorescence spathe and floral bract vestiture; and absence or presence and type and amount of pubescence on perianth tube and ovary. Recognition of just one hypervariable Malesian species does not adequately reflect the biological situation. I propose the following: recognition of *P. borneensis* Stapf and the west New Guinean *P. novo-guineensis* Gibbs, currently subsumed in *P. lowii* Stapf; addition of a second species in Papua New Guinea, *P. inflexa* Goldblatt; and treatment of the Sumatran highland plants as *P. sumatrensis* Goldblatt from Indonesia. Philippine plants from Mindoro match none of these and represent another species, *P. philippinensis* Goldblatt. Lectotypes are designated for the two names *P. lowii* and *P. novo-guineensis*. This taxonomy awaits provenance of flowers with well-preserved perianths of all but *P. lowii* and *P. borneensis* and capsules and seeds of *P. philippinensis*, but are unlikely to alter this treatment. Floral differences among most *Patersonia* species are small, except for the vestiture on tepals and tube visible in many of the available specimens, and for the most part involve only modest differences in size and color of the tepals.

Key words: Indonesia, Iridaceae, Malaysia, Malesia, Papua New Guinea, *Patersonia*, The Philippines, Sumatra, West Papua.

The Australasian and Malesian *Patersonia* R. Br. (Iridaceae), the only genus of Patersonioideae (Goldblatt et al., 2008), is centered in Australia, where 18 species are recognized (Cooke, 1986; Keighery, 1990). One species, *P. neocaledonica* Goldblatt & J. C. Manning, is restricted to New Caledonia (Goldblatt et al., 2011), and one more, *P. lowii* Stapf from Sabah, Malaysia, is currently recognized in the Malesian archipelago, but two more have been described: *P. borneensis* Stapf, from Mt. Kinabalu, Borneo, and *P. novo-guineensis* Gibbs, from western New Guinea. Both latter names were reduced to synonymy in *P. lowii* by Geerinck (1977) for the *Flora Malesiana*. This treatment was followed by Van Royen (1979) and Beaman and Beaman (1998), respectively, in their floristic accounts for New Guinea and Mt. Kinabalu, Borneo.

Patersonia comprises mostly evergreen, tufted perennials with creeping rhizomes, which bear a 2-ranked fan of unifacial leaves and produce unbranched, leafless flowering stems seasonally, each bearing a terminal inflorescence, a binate rhipidium (Goldblatt, 1990; Goldblatt & Manning, 2008). The deciduous geophyte *P. babianoides* Benth. has a single leaf and a fleshy rhizome that produces annual, cormlike segments. Just three species, *P. glabrata* R. Br., *P. pygmaea* Lindl., and *P. spirafolia* Keighery, have woody, leafy stems, a habit thus resembling a low shrub. All Malesian populations of *Patersonia* have the more common tufted growth form.

Flowers of all *Patersonia* species are surprisingly similar: the inflorescence, a binate rhipidium, is enclosed by a pair of large leafy bractlike structures, the spathes. Individual flowers, each subtended by a dry, membranous bract, are sessile, have a narrowly ellipsoid ovary about half as long as the spathes and a slender tube that serves the function of a pedicel, raising the flower from the spathes. The flowers are fugaceous, lasting just a morning each, and have large, spreading outer tepals colored blue to mauve, sometimes white or partly white with a blue center. The inner tepals are reduced in size, most often represented by linear spreading cusps, or are absent. The Australian *P. umbrosa* Endl. and the New

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Caledonian *P. neocaledonica* are exceptional in having lanceolate inner tepals about one third as long as the outer tepals. *Patersonia umbrosa* var. *xanthina* (F. Muell.) Domin stands out in having yellow flowers. The filaments are partly to fully united in a column, and the style divides opposite the anther apices, or sometimes beyond them, into three broad stigmatic lobes. The capsular fruits are ellipsoid and fully dehiscent but are retained within the spathes.

Except for Stapf's (1894) careful analysis of collections of the two species on Mt. Kinabalu, Borneo (now Sabah, Malaysia), *Patersonia* in the Malesian area has received little critical study. Part of the reason is that collections have been slow to accumulate, and none that I have seen include carefully pressed flowers. Despite these handicaps, there are several distinctive characters among the available collections at several herbaria (mainly CANB, GH, K, L) that cast doubt on their treatment as a single species.

Of the two named species from Borneo, both on the Mt. Kinabalu massif, *Patersonia borneensis* and *P. lowii*, the first is relatively tall, reaching to 60 cm (Table 1), and has leaves exceeding the stem and rhipidia, and the second, about half as tall, has a stem about as long as the leaves, sheathed by the uppermost leaf close to the base of the rhipidium. Leaves of *P. borneensis* are closely ribbed, lack marginal tomentum but are usually minutely papillate when viewed at high magnification (above 20×). In contrast, in *P. lowii*, which has striate leaves (when dry), the margins are usually brown-tomentose, and the leaf surface lacks papillae. The keels of the outer rhipidial spathes and margins of some of the floral bracts are also sparsely brown-tomentose, whereas the spathes and bracts of *P. borneensis* are glabrous.

The flowers of the two species, carefully dissected by Stapf and illustrated in his 1894 paper, are similar, but those of *Patersonia borneensis*, described by collectors as purplish white, lack inner tepals and have entire, obovate stigmatic lobes. Flowers of *P. lowii*, evidently blue or purple, are shown in his drawing as having vestigial, cusplike inner tepals. Stapf, however, was uncertain on this point, and in his description (1894: 241) used the words "lobi … nullo (?)" and described minutely crenulate stigmatic lobes. The slender perianth tube is 25 mm (1 inch) long in *P. borneensis* and 22 mm ("11 lin[es]") long in *P. lowii*. Not noted by Stapf, the perianth tube of *P. borneensis* bears scattered branched hairs (Table 1).

Plants from western New Guinea, now West Papua, Indonesia, and adjacent western Papua New Guinea, described by Gibbs (1917) as *Patersonia novo-*

Table 1. Comparison of critical taxonomic characters of Malesian *Patersonia* species.

	Leaf dimensions and surface	Leaf margins	Stem flexure, height and width	Spathe keels and floral bract margins	Perianth tube tomentum
P. borneensis Stapf	42–60 cm × (3–)4–6 mm; ribbed, papillate	smooth	straight; 42–55 cm × ca. 1.5 mm	smooth	scattered multicellular hairs
P. lowii Stapf	15–30 cm × 3–4 mm; striate, smooth	densely brown to brown-tomentose	straight; 15–30 cm × ca. 1.5 mm	brown-tomentose on spathe keels and some bract margins	somewhat smooth or sparsely white-hairy below
P. inflexa Goldblatt	10–22 cm × 2–3(–4) mm; striate, smooth	white, sometimes brown-ciliate	usually strongly flexed; 12–20 cm × ca. 1.5 mm	smooth	brown-tomentose in lower half
P. novo-guineensis Gibbs	15–30 cm; striate, smooth	brown-tomentose	straight; (5–)10–20 cm × ca. 2 mm	brown-tomentose on spathe keels and some bract margins	brown-tomentose in lower half
P. philippinensis Goldblatt	90–120 × 2.0–3.5 mm; smooth	slightly thickened, smooth	straight, 10–12 cm × 0.8 mm	smooth	unknown
P. sumatrensis Goldblatt	12–25 cm; striate-smooth	smooth	weakly flexed; 18–35 cm × ca. 1.5 mm	smooth	smooth

guineensis, resemble *P. lowii* in general aspect and have, like that species, brown-tomentose leaf margins and sometimes tomentose spathe keels and bract margins or tips. Gibbs (1917: 101) distinguished her species by the particularly conspicuous brown marginal tomentum ("matted branched hairs") and white or pale mauve flowers. The inner tepals are lacking, and the outer tepals have a conspicuous apical tuft of hairs. Unlike *P. lowii*, the perianth tube usually bears a tomentum of dark brown, branched hairs, denser in the lower half of the tube.

Populations from eastern Papua New Guinea have flowers described as mauve or blue, the outer tepal tips lack a terminal tuft of hairs, and although plants superficially resemble *Patersonia lowii* and *P. novo-guineensis* in their low stature, the uppermost leaf reaches only to the middle of the stem, which is flexed outward above the sheath of this leaf. The feature is so marked that the stem was noted by one collector (*Woods 2627*, holotype, NSW) as "curved into a horizontal position." The leaf margins in all collections that I have seen are minutely pale-ciliate, occasionally turning brown, but the spathes and bracts are smooth. Notable in these plants are branched, dark brown hairs at the distal end of the ovary and lower perianth tube, densest near the ovary apex.

Plants from northern Sumatra, on Gunung Leuser (also called Mt. Loiser) in the Gunung Leuser Nature Reserve, represent another variant. They have the low stature and general appearance of *Patersonia lowii*, but the leaves and spathes are glabrous, lacking even a trace of marginal cilia. However, the stems are flexed above the sheath of the uppermost leaf, but the feature is less pronounced than in the eastern Papua New Guinea plants. Flower color was variously described by collectors as lilac, lilac-blue, or bluish.

Last, *Patersonia* has also been recorded from the Philippines, where Merrill (1907) identified a collection from Mt. Halcon, Mindoro, as *P. lowii*. Recently, the genus has been reported from Mt. Hamiguitan, Mindanao (Amoroso et al., 2009), also as *P. lowii*. The Mindoro plants are smaller than any from elsewhere in Malesia, no more than 15 cm high, and the leaf margins, spathe keels, and floral bract margins are smooth, thus unlike those of *P. lowii*. No specimens of the Mindanao plants were evidently collected, or they have not been made available to me despite requests.

The range of morphological variation among the populations of *Patersonia* in the Malesian Archipelago is greater than one would expect in a single species, and I have no hesitation in recognizing all three of the Malesian species described to date. I also consider it advisable to accord species rank to plants from Sumatra (*P. sumatrensis* Goldblatt), eastern Papua New Guinea (*P. inflexa* Goldblatt), and Mindoro (*P. philippinensis* Goldblatt). They can readily be keyed out on vegetative features, and these characters are consistent with those floral or fruit differences that can be seen in the available specimens, notably ovary and perianth tube vestiture.

Review of Morphology in Malesian *Patersonia*

Leaves are narrowly sword-shaped to linear. The narrow hyaline margins are smooth in *Patersonia borneensis*, *P. sumatrensis*, and *P. philippinensis*, white to brown ciliate in *P. inflexa*, and brown-tomentose in *P. lowii* and *P. novo-guineensis*. When dry, the leaves are striate (perhaps an artifact of drying, the ridges merely representing the leaf veins) and smooth, except in *P. borneensis*, which has ribbed leaves and a papillate surface visible only at greater than 25× magnification. The leaves are typically about as long as the stems, sometimes exceeding them, notably so in *P. borneensis* and *P. philippinensis*. Stems are erect or, in *P. inflexa* and to a lesser extent in *P. sumatrensis*, flexed above the sheathing portion of the uppermost leaf, leaving the stem and rhipidium inclined to almost horizontal. The rhipidial spathes are noted in some collections to be colored shades of brown (purple-brown, orange-brown, red-brown), and I assume brownish-colored spathes for all Malesian species (also a feature of 12 Australian species). The keels of the spathes of *P. lowii* are partly brown-tomentose, especially toward the tips. In *P. novo-guineensis*, the bract tips bear a tuft of branched hairs.

Flowers are typical of the genus, always shades of blue-mauve to lilac or described as sometimes white. The inner tepals are said to be absent in *Patersonia borneensis*, but drawings for *P. lowii* by Stapf (1894) show vestigial inner tepals represented by linear cusps ca. 5 mm long. I assume the inner tepals are vestigial (perhaps absent) in the remaining Malesian species. The perianth tube of *P. inflexa* and *P. novo-guineensis* bears a dense tomentum of branched, brown hairs. In *P. sumatrensis*, the perianth tube is smooth; in *P. borneensis* and *P. lowii*, it has a few, scattered hairs, white or brown in color. Details of the androecium and gynoecium are known only for *P. borneensis* and *P. lowii* from Stapf's (1894) drawings of his careful dissections. The filaments are completely united in a column, and the ovary is smooth, or in *P. inflexa* bears branched hairs.

The capsules are smooth—or in *Patersonia inflexa*, tomentose near the apex—and show the outline of the seeds at maturity. Seeds, known in four species, are

ellipsoid, dark brown (not black as described by Stapf [1894], for *P. borneensis*), and shiny, and show the outlines of elongate surface cells below the translucent cuticle. A flattened, white aril, or perhaps more correctly a caruncle (defined as an aril-like outgrowth arising from the mouth of the micropyle, the apparent condition in *Patersonia*), is present at the micropylar end, largest in *P. sumatrensis* and twisted and appressed, flattened and twisted in *P. borneensis*, round or elongate and curved in *P. novo-guineensis*, and in *P. inflexa*, tapering, distally linear and appressed. Seeds of *P. inflexa* have a small hook at the micropylar end. Only one or at most two collections of any species have mature seeds, so variation for caruncle shape cannot be assessed. Seeds of *P. lowii* and *P. philippinensis* are unknown.

Seeds of six Australian species of *Patersonia* are reported to have white, so-called arils (Cooke, 1986) and have been described either as cylindrical with linear appressed arils (*P. juncea* Lindl., *P. pygmaea*), compressed-ovoid and brown (*P. inaequalis* Benth.), or black (*P. fragilis* (Labill.) Asch. & Graebn., *P. drummondii* F. Muell. ex Benth., *P. glabrata*). The aril color, white, is noted only in *P. fragilis*. Except for the absence of an aril (more accurately, the caruncle), the seeds of *P. occidentalis* R. Br. (illustrated in Cooke, 1986: frontispiece) closely resemble those of the Malesian species in color, texture, and shape (described as compressed-ovoid, thus equivalent to the term "ellipsoid," as used herein).

IUCN Red List category. Although I have no personal field knowledge of *Patersonia*, I offer the following observations on the conservation status (sensu IUCN, 2001) of the genus in the Malesian area. All populations grow at high elevations, mostly above 2000 m, and away from human habitation, and thus are minimally affected by human activity. Populations in Borneo, the Philippines (both Mindanao and Mindoro), and Sumatra are in official nature reserves, national parks, or conservation zones. In New Guinea, *P. novo-guineensis* is relatively widespread, but *P. inflexa* appears to be a relatively narrow endemic. Nevertheless, no species is currently under any conceivable threat. Like other high mountain species, however, global warming may open their habitats to species today confined to lower, warmer elevations, increasing competition for habitat and possibly driving *Patersonia* populations to higher elevations.

Geographic Observations

Populations of *Patersonia* in Malesia are confined to the higher mountains of the archipelago. All species occur at elevations above 1500 m and, except for *P. lowii*, above 2000 m. All six species are allopatric and except for *P. borneensis* and *P. lowii* (both on Mt. Kinabalu but at different elevations) are isolated by substantial distances of some hundreds of kilometers. The Philippines sites for the genus on Mindoro and Mindanao are some 900 km from the next nearest station for the genus, Mt. Kinabalu. Gunung Leuser in northern Sumatra is over 2000 km from Mt. Kinabalu and even farther from the nearest New Guinea population. Such long-distance dispersal is remarkable in the Iridaceae where few genera, including *Patersonia*, have adaptations for dispersal over long distances. *Patersonia* seeds are 2–3 mm long in the Malesian species known for this organ and bear small white caruncles, which I infer are adaptations for local dispersal by ants. The center of diversity for *Patersonia* is undoubtedly Australia, where it is widespread, but it is most diverse in Western Australia (Cooke, 1986). It seems most reasonable to postulate dispersal from Australia, first to New Guinea sometime after that landmass rose above sea level in the Middle Miocene, and then to high mountains in Mindanao and Borneo, some 1500 km distant, reaching Sumatra last, the most distant from any recorded station for the genus. Other high mountains in Malesia may well harbor *Patersonia*. Those on several islands—notably Celebes, Java, and Timor—reach elevations above 2500 m. There are no comparable radiations in Iridaceae, but the predominantly African genera *Gladiolus* L. (ca. 265 spp.), *Moraea* Mill. (ca. 210 spp.), and *Romulea* Maratti (ca. 90 spp.) each have species throughout sub-Saharan Africa and just a handful in Eurasia; these are thought to be descended from single introductions, at least in *Gladiolus* and *Moraea*, from ancestors in southern Africa (Goldblatt et al., 2002; Valente et al., 2011). The small morphological differences among the Malesian species of *Patersonia* likewise suggest a single introduction from the south. Based on molecular clock estimates, *Patersonia* diverged from its immediate sister lineage ca. 55 million years ago (Ma) (Goldblatt et al., 2008). The genus was thus established in Australia long before the Malesian Archipelago was available for colonization. Again based on morphology, dispersal of *Patersonia* to New Caledonia was likely an independent event.

Taxonomic Treatment

Patersonia R. Br. in Ker Gawl., Bot. Mag. 26: tab. 1041. 1807, nom. cons., non *Genosiris* Labill., Nov. Holl. Pl. 1: 13. 1805. TYPE: *Patersonia sericea* R. Br.

KEY TO THE MALESIAN SPECIES OF *PATERSONIA*

1a. Abaxial and sometimes adaxial leaf margins above the level of the sheath densely tomentose with dark brown, branched hairs; distal parts of spathe keels and often floral bract tips or distal margins hairy.
  2a. Outer tepals with a tuft of branched hairs at apices; perianth tube usually densely tomentose or sometimes sparsely hairy to ± smooth (perhaps by abrasion), with brown, branched hairs ..... 4. *P. novo-guineensis*
  2b. Outer tepals without hairs at tepal apices; perianth tube sparsely hairy or evidently smooth ..... 3. *P. lowii*
1b. Leaf margins smooth or bearing minute translucent or brown cilia; spathe keels and bract margins and apices glabrous.
  3a. Plants small, mostly 8–12 cm high; leaf blades 2.0–3.5 mm wide; inner rhipidial spathes 23–30 mm ... . 5. *P. philippinensis*
  3b. Plants medium-sized to relatively large, mostly 18–60 cm high; leaf blades 2–6 mm wide; inner rhipidial spathes 35–50 mm.
    4a. Leaf blades closely ribbed and minutely papillate (30× magnification); flowering stem ± erect throughout and shorter than leaves; perianth tube sparsely hairy (or smooth due to abrasion)..... ..... 1. *P. borneensis*
    4b. Leaf surface smooth or occasionally obscurely papillate (30× magnification) and striate to obscurely ribbed when dry; perianth tube smooth or densely woolly hairy.
      5a. Perianth tube and usually distal part of ovary with a dense tomentum of branched, brown hairs; stem flexed outward above sheath of uppermost leaf, nearly horizontal; leaf margins bearing white or occasionally brown cilia ..... 2. *P. inflexa*
      5b. Perianth tube and ovary smooth; stem erect or slightly flexed above sheath of uppermost leaf; leaf margins lacking cilia ..... 6. *P. sumatrensis*

1. Patersonia borneensis Stapf, Trans. Linn. Soc. London, Bot., ser. 2, 4: 242. 1894. TYPE: Malaysia. Sabah: Mt. Kinabalu, Temburungo, 7700 ft. [ca. 2300 m], 1892; *G. D. Haviland 1179* (holotype, K [barcode] 000523994!; isotype, K [barcode] 000523995!).

Tufted perennials 35–60 cm high; stems compressed, oval in section, 42–55 cm, ca. 1.5 mm diam., ± erect throughout, shorter than leaves. Leaves many, basal, usually slightly exceeding stems; blades 4–6 mm wide, closely ribbed, minutely papillate (30× magnification), margins smooth; the uppermost leaf sheathing stem to about midstem, the apex rarely reaching base of spathes. Rhipidial spathes 36–50 mm long, subequal or inner slightly longer, brownish purple, keels and margins smooth; floral bracts dry-membranous, protruding a short distance from spathes, margins smooth. Flowers pale lavender to blue-purple (also described as whitish purple); perianth tube ca. 25 mm, with sparse, branched hairs especially in lower half or smooth due to abrasion; outer tepals ovate, ca. 15 mm, inner tepals lacking; filaments united in a column ca. 1 mm; anthers ca. 2 mm long; ovary ellipsoid, 18–23 mm, smooth; style dividing at apex anthers, stigma lobes obovate. Capsules ellipsoid, 20–25 mm, smooth, narrowed in proximal 5 mm and without seeds; seeds ellipsoid, dark brown, shiny, 2.5–3 × 1 mm, micropylar caruncle white, flattened and twisted, ca. 0.5 mm long. Flowering mainly in December to April.

Discussion. Restricted to high elevations on the Mt. Kinabalu massif in Sabah, Malaysia, *Patersonia borneensis* stands out in being the tallest of the Malesian species of the genus, as tall as 60 cm. The leaves, which exceed the flowering stems, have smooth margins, and the spathe keels and margins and the floral bract margins likewise lack vestiture of any kind (Table 1). The leaves are, however, closely ribbed and visibly papillate under greater than 25× magnification, unique for the Malesian species. This stands in marked contrast to the other Mt. Kinabalu species, *P. lowii*, which has brown-ciliate to brown-tomentose leaf margins, the leaf surface also striate but smooth, usually the keels and upper margins of the spathes brown-ciliate to tomentose, and floral bracts with margins and tips brown-tomentose. The flowers of the two species are broadly similar, *P. borneensis* having the slender perianth tube ca. 25 mm long and bearing scattered branched hairs in the lower half, whereas *P. lowii* has a perianth tube ca. 22 mm long, smooth or with scattered, apparently unbranched hairs in the lower half. The stigma difference noted by Stapf, smooth in *P. borneensis* but crenulate in *P. lowii*, may be significant but should be confirmed when more flowering specimens become available, as should the possible presence of vestigial inner tepals in the latter.

The above differences provide ample grounds for regarding *Patersonia borneensis* as distinct from *P. lowii*. In addition, current records of *P. borneensis* are all from higher elevations than *P. lowii*, 2000 m and above (2200–2750 m), whereas the few records of *P. lowii* are from no higher than 1675 m. This suggests that the two species have different ecology and habitat preferences.

Additional specimens examined. MALAYSIA. **Sabah:** Mt. Kinabalu, E shoulder, on ridge in dry places, *W. L. Chew, E. J. Corner & A. Stainton 996* (K, L); upper

Kinabalu, *J. Clemens & M. S. Clemens 30061* (GH, K, L, UC); *J. Clemens 50981* (NY); upper Kinabalu, Kamberanga, *J. & M. S. Clemens 30951* (NY); *M. S. Clemens 10545* (UC); Kinabalu, Kamburangah, *L. S. Gibbs 3124* (BM, K); Mt. Kinabalu, Garulu spur, open places in mossy forest, *J. & M. S. Clemens 51034* (BM, GH, K, L, UC); Kalabit Highlands, Mt. Murud, slope with open shrubby vegetation, *H. P. Nooteboom & P. Chai 20256* (BISH, CANB, K, L).

2. Patersonia inflexa Goldblatt, sp. nov. TYPE: Papua New Guinea. Milne Bay: Mt. Dayman area, Donana, 7500–8000 ft. [2285–2440 m], subalpine grassland with moss, forest edge, 24 July 1968 (fl.), *P. J. B. Woods 2627* (holotype, NSW!; isotypes, GH!, K!, L!).

Plantae *Patersoniae lowii* Stapf similes, sed ab ea foliis 2–3(–4) mm latis marginibus minute ciliatis, spathis subaequalibus 35–43 mm longis carinis marginibusque laevigatis, tubo perianthii ca. 25 mm longo dense tomentoso atque ovario ca. 14 mm longo distinguuntur.

Tufted perennials 15–22 cm high; stems compressed, reddish brown, oval in section, 12–20 cm × ca. 1.5 mm, flexed outward above sheath of uppermost leaf and nearly horizontal. Leaves 8 to 10 per shoot in 2 ranks, basal, usually slightly shorter than flowering stem (or slightly longer); blades 2–3(–4) mm wide, when dry closely striate, smooth (30× magnification), margins translucent (white when dry) or sometimes brown-ciliate, uppermost leaf sheathing ca. lower half of stem, blade tip not reaching spathes. Rhipidial spathes reddish brown, subequal, 35–43 mm long, inner 2–3 mm longer than outer, with broad, brown-translucent margins, keels and margins smooth; floral bracts dry-membranous, smooth. Flowers mauve-blue (also described as purple), darker in center; perianth tube ca. 25 mm, densely covered in lower half with branched, brown hairs, denser tomentum toward base, usually extending on distal ovary; outer tepals narrowly ovate, ca. 15 × 7 mm; filaments united in a column ca. 1 mm; anthers ca. 2 mm; ovary ellipsoid, ca. 14 mm, with a tuft of branched hairs near apex; style dividing at apex of anthers, stigma lobes unknown. Capsules ellipsoid, 18–25 mm long, smooth, narrowed in proximal 5 mm and without seeds; seeds ellipsoid, smooth, glossy dark brown, ca. 2 × 1 mm, hooked at micropylar end, micropylar caruncle white, small, flattened, tapering, distally sublinear and appressed. Flowering recorded in June, July, and October.

Discussion. *Patersonia inflexa* is a relatively narrow endemic of the high mountains of eastern Papua New Guinea and, like other Malesian species of *Patersonia*, grows in grassy moorland and subalpine grassland in open habitats. The taxon is most easily distinguished by the characteristic flexed flowering stem, sometimes bent almost horizontally above the sheathing part of the terminal leaf. Unlike the other New Guinea species, *P. novo-guineensis*, the leaves are sparsely ciliate, and the spathe keels and floral bracts are completely smooth. The two New Guinea species share a woolly tomentose perianth tube, the pubescence extending on to the upper part of the ovary in *P. inflexa*. Although seeds are available for few specimens of any Malesian species, those from *Brass 22259* and *Cruttwell 553* show a distinctive hooked micropylar end, not evident in one seed sample each of *P. borneensis*, *P. novo-guineensis*, and *P. sumatrensis*.

P. F. Stevens & J. F. Veldkamp s.n., a collection included here, consists of short, tufted plants ca. 8 cm high with the leaves exceeding the stems, which are straight and sheathed by the uppermost leaf to the base of the spathes. Collected at 3500 m on Mt. Suckling, Papua New Guinea, it may represent a dwarfed, high-elevation variant of *Patersonia inflexa*. More material is needed to investigate this question in more detail.

Paratypes. PAPUA NEW GUINEA. **Milne Bay:** Mt. Maneau, grassy moorland, slopes just below summit, *N. G. Cruttwell 553* (fr.) (K); Mt. Donana, mtn. top moorland, *N. G. Cruttwell 931* (K); Mt. Dayman, Maneau Peak, 2750 m, common in grassland, *L. J. Brass 22259* (fr.) (CANB, K, U); Goropu Mtns. (Mt. Suckling), subalpine grassland, sunny rocky slopes and screes, *J. F. Veldkamp & P. F. Stevens 5636* (BISH, CANB, L, NSW, PNG); Raba Raba, Mt. Suckling complex, S side of Goe Dendeniwa, margins of ultramafic bedrock, *P. F. Stevens & J. F. Veldkamp s.n.* (CANB-244089, L).

3. Patersonia lowii Stapf, Trans. Linn. Soc. London, Bot., ser. 2, 4: 241. 1894. TYPE: Malaysia. Sabah: Mt. Kinabalu, NW face, 5000 ft. [ca. 1520 m], s.d., *H. Low s.n.* (lectotype, here designated, K [barcode] 000523997!).

Tufted perennials 15–30 cm high; stems compressed, oval in section, 15–30 cm × ca. 1.5 mm wide. Leaves ca. 9 to 12 per shoot, slightly shorter or slightly longer than flowering stem, 15–30 × 3–4 mm, when dry closely striate, smooth (when viewed above 25× magnification), margins densely brown-ciliate to brown-tomentose, uppermost leaf sheathing fertile stem almost to base of rhipidium, the free blade portion exceeding the spathes. Rhipidial spathes subequal, 36–40 mm long, color unknown, usually keels (not in *Clemens & Clemens 32931*) and often upper margins brown-ciliate to brown-tomentose, lower spathe margins broadly dry-membranous; floral bracts dry-membranous, often with margins and tips brown-tomentose. Flowers blue to purple; perianth

tube ca. 22 mm, evidently smooth or sparsely hairy in lower half; outer tepals obovate, 12–14 × 8–9 mm, without hairs at tepal apex; inner tepals ?short, linear cusps ca. 5 mm (from drawing by Stapf, 1894) or ?lacking; filaments united in a column; anthers ca. 3 mm; ovary ellipsoid, ca. 25 mm, smooth; style dividing at apex of anthers, stigma lobes somewhat obovate, minutely crenulate. Capsules and seeds unknown. Flowering recorded in November and March.

Discussion. A narrow endemic of Mt. Kinabalu in Borneo, *Patersonia lowii* is evidently restricted to the Marai Parai (also Maripari) spur. Moderate in height, only 15–30 cm tall, it is recognized by the leaves with brown-ciliate to brown-tomentose leaf margins, a smooth leaf surface, closely striate when dry, and similarly brown-ciliate to brown-tomentose spathe keels and floral bracts. The flowers hardly differ from those of other Malesian species of the genus except for the almost smooth perianth tube, at best sparsely hairy in the lower half, a feature contrasting markedly with *P. novo-guineensis* and *P. inflexa*, which have a woolly perianth tube, and the former also has a tuft of brown hairs on the tepal apices. Other apparently minor floral differences noted above under *P. borneensis* remain to be confirmed. Leaves, spathes, and floral bracts of *P. sumatrensis* lack indumentum of any kind, and leaves of *P. inflexa* are only sparsely ciliate.

Geerinck (1977) included all *Malesian* collections of *Patersonia* in *P. lowii*, noting that, not only was the species (in his broad circumscription) variable for the indumentum, but disjunct populations were not uniform for the character. To the contrary, the Sumatran populations, now *P. sumatrensis*, are quite uniform, and the West Papuan *P. novo-guineensis* is only moderately variable once the eastern Papua New Guinea plants I refer to as *P. inflexa* are treated as a separate species. There is also no overlap in the critical features of *P. borneensis* and typical *P. lowii* although both grow on Mt. Kinabalu. The shorter stature, smooth leaf surfaces, brown-tomentose leaf margins and spathe keels, almost smooth to sparsely hairy perianth tube, and possibly differently shaped stigma lobes readily separate the two. The slightly larger flowers of *P. borneensis*, said to lack inner tepals (probably present in *P. lowii*), may also serve to separate them, but material is too limited at present to rely on this character. It is also significant that records of *P. lowii* are from 1520 to 1675 m, whereas the recorded range of *P. borneensis* is from 2200 to 2750 m. As lectotype for *P. lowii* I designate *Low s.n.*, the better preserved of the two syntypes on which the species was based. Both syntypes are on the same sheet at Kew, *Low s.n.* at left, and *G. D. Haviland 1259* (K [barcode] 000523996) at right.

Additional specimens examined. MALAYSIA. **Sabah:** Mt. Kinabalu, Marai Parai spur, *J. Clemens 248* (GH); *J. Clemens & M. S. Clemens 32931* (K, L, NY); *s.n.* (BM).

4. Patersonia novo-guineensis Gibbs, Contr. Phytogeog. Fl. Arfak Mts., 101. 1917. TYPE: Indonesia. Irian Jaya [as Netherlands New Guinea]: Arfak Mtns., Koebré Ridge, open burnt places on summit, 9000 ft. [ca. 2740 m], Dec. 1913 (fl., fr.), *L. S. Gibbs 5600* (lectotype, designated here, BM!; isolectotypes, K [barcode] 000291969!, L!).

Patersonia novo-guineensis var. *auriculata* Went, Nova Guinea 114. 1924. TYPE. Indonesia. Irian Jaya [as Netherlands New Guinea]: Mamberamo River area, summit of Mt. Doorman, 3320 m, 20 Oct. 1920, *H. J. Lam 1670* (type, L).

Tufted perennials 15–30 cm high; stems compressed, oval in section, (5–)10–20 cm × ca. 2 mm. Leaves usually 8 to 12 per shoot in 2 ranks, ca. as long as or exceeding stems by up to 5 cm, (2–)4–6 mm wide, when dry closely striate, smooth (30× magnification), abaxial and sometimes adaxial margins hyaline and densely brown-tomentose. Rhipidial spathes 28–38 mm long, subequal, inner up to 2 mm longer, spathe margins broadly translucent brown, outer usually brown-tomentose distally, outer spathe keels often densely tomentose; floral bracts dry-membranous, slightly shorter to ca. as long as spathes, some occasionally tipped with brown hairs. Flowers white or pale blue-mauve (also described as purple or violet); perianth tube ca. 20 mm, densely tomentose with branched brown hairs or sometimes sparsely hairy to ± smooth (perhaps by abrasion) (*Kanechira & Hatusima 13663, 13691*); outer tepals ca. 15 mm, with a tuft of hairs at apices, inner tepals lacking (Gibbs, 1917); filaments united in a column ca. 1.5 mm; anthers 2–3 mm; ovary sessile, ellipsoid, evidently 13–15 mm, smooth; style dividing at apex of anthers, stigma lobes narrowly oblong. Capsules ellipsoid, 16–20 mm, smooth, narrowed in proximal 5 mm and without seeds; seeds ellipsoid, smooth, glossy dark brown, ca. 2 × 1.3 mm, micropylar caruncle white, flattened, round or elongate and curved, ca. 0.8 mm long. Flowering in September to June.

Discussion. First collected in 1915 in the Arfak Mountains of western New Guinea, now West Papua, Indonesia, *Patersonia novo-guineensis* is now understood to extend from Mt. Angi in the west to Mt. Stolle in adjacent western Papua New Guinea to the east,

always at high elevations, between 2000 and 3320 m. The species is recognized by the heavily brown-tomentose leaf margins, this accompanied by brown-tomentose spathe keels and lower margins, and floral bracts sometimes tipped with brown hairs. Only *P. lowii* has these organs with comparably dense vestiture. *Patersonia novo-guineensis* has in addition a perianth tube ca. 20 mm long, the lower part of which is densely covered with branched, brown hairs. The tepal tips also bear an apical tuft of hairs, a character unique in *Patersonia*. In *P. lowii* the perianth tube is ca. 25 mm long and smooth or at best sparsely short-hairy.

Like other species of Malesian *Patersonia* for which this is known, the seeds of *P. novo-guineensis* have a small white caruncle. Seeds of *P. lowii* are unknown. The second New Guinean species of the genus, *P. inflexa*, also has carunculate seeds, but the seeds, still poorly documented, are hooked at the micropylar end. This species also has a tomentose perianth tube, perhaps indicating shared ancestry, but it differs markedly in other features, including the inflexed flowering stem always exceeding the leaves, the smooth spathe margins and keels, and ciliate leaf, rather than margins of *P. novoguineensis*, which are conspicuously brown-tomentose.

One of the syntype collections of the plant that was subsequently identified as *Patersonia novo-guineensis* var. *auriculata* by Went (1924), *Lam 1670*, was examined by Van Royen (1979), who concluded that it was a species of Cyperaceae. A duplicate at L, designated as an isotype in unknown hand, is a poorly preserved specimen of *P. novo-guineensis* lacking flowers or intact fruit, although the decaying inflorescence spathes and leaves show the characteristic tomentose keels or margins of this species. The flowering stem is unusually short, half as long as the leaves, but such shortened stems are known in the species. For example, a collection from Angi in the Arfak Mountains, *Kanechira & Hatusima 13663*, consists of plants with one short stem to 5 cm and a second, normal-looking stem 12.5 cm long. The isotype (*Lam 1670*) does not show details of the perianth noted in the protologue of variety *auriculata* (perianth segments 15 mm long). The location of other duplicates of the type of variety *auriculata* is unknown to me, but the taxon cannot be a species of Cyperaceae with tepals as described in the protologue.

Additional specimens examined. INDONESIA. **Irian Jaya [West Papau]:** Manokwari, Iray, path to summit of Mt. Koebré, subalpine forest *R. J. Johns et al. 8037* (GH, K); Arfak Mtns., Angi, *R. Kanechira & S. Hatusima 13691* (GH), *13663* (GH, K); Tamrau Range E, Wamsuf area above Waumi River, *P. van Rooyen & H. Sleumer 7202* (K, L); Angi, top of Kobrei to Gita Lake, *E. A. Widjaja EAW 4341* (CANB, K); Mt. Kobreimot (Koebré), WSW from Testega, Anggi Lakes, *H. Sleumer & Vink BW14172* (BISH, CANB, L); Arfak Mtns., Lake Angi, *K. Gjellerup 1209* (K, L). PAPUA NEW GUINEA. **Morobe:** Mt. Amungwiwa, alpine grassland below summit, 13 June 1976, *P. van Royen 11128* (BISH, K, L). **West Sepik:** Mt. Stolle, ridge on W side of mtn., 2500 m, 2 Sep. 1994, *J. C. Regalado & Katik 1302* (GH).

5. Patersonia philippinensis Goldblatt, sp. nov. TYPE: The Philippines. Mindoro: Mt. Halcon, 14 Apr. 1991, *B. J. Stone et al. 16390* (holotype, BRIT!; isotype, BISH!).

Plantae *Patersoniae lowii* Stapf similes, sed ab ea caule 9–12 cm × ca. 0.8 mm lato, foliis 90–120 × 2.0–3.5 mm marginibus laevigatis, spathis inaequalibus interna 23–30 mm longa externa 20–24 mm longa atque carinis marginibusque spatharum et marginibus bractearum laevigatis distinguuntur.

Tufted perennials mostly 8–12 cm high; stems straight, compressed, oval in section, shorter than leaves, 10–12 cm × ca. 0.8 mm, enclosed by sheath of uppermost leaf to or almost to the base of spathes in fertile stems. Leaves several per shoot in 2 ranks, basal, exceeding flowering stems, 90–120 × 2.0–3.5 mm, leaves when dry obscurely striate, surface (with 20× magnification) and margins smooth. Rhipidial spathes unequal, inner 23–30 mm, outer 20–24 mm, keels and margins smooth; floral bracts dry-membranous, margins smooth. Flowers mauve or blue; no other floral or fruit details known. Flowering recorded in April.

Discussion. Although *Patersonia* has long been known from the Philippines, first from Mt. Halcon, Mindoro (Merrill, 1907), and recently from Mt. Hamiguitan, Mindanao (Amoroso et al., 2009), I have seen only one collection, from Mindoro. Evidently Merrill's collection from Mindoro, made in 1906, is lost, and there is apparently no voucher for the Mindanao record. Nevertheless, at least the Mindoro plant is clearly not *P. lowii*, the species to which it was provisionally assigned by Merrill. The leaves, no more than 15 cm high, consistently longer than the flowering stems, and 2–3 mm wide (vs. 3–4 mm wide in *P. lowii*), have smooth margins, and the spathe keels and margins and floral bracts are also smooth, thus unlike the prominently brown tomentum on these organs in *P. lowii*. Similarly, the subequal spathes of *P. lowii*, 36–40 mm long, are larger than the unequal spathes of *P. philippinensis*, in which the inner are 23–30 mm long and the outer are 20–24 mm long. Unfortunately, few floral and no fruit details are known, and little more can be said about the possible relationships of this new species. It would be

useful to examine *Patersonia* from Mt. Hamiguitan as it is some 800 km from Mt. Halcon, but both peaks are about 900 km from the next nearest site for the genus, the Kinabalu Massif. Given the geographic patterns of speciation in *Patersonia*, the Mt. Hamiguitan plants may well be a separate species.

6. Patersonia sumatrensis Goldblatt, sp. nov. TYPE: Indonesia. Sumatra: Gunung Leuser National Park, Gunung Leuser (as Mt. Losir), Gajolands, acid, stony open ground in mtn. heathland, 2100–2250 m, 29 Jan. 1937, *C. C. van Steenis 8444* (holotype, L!; isotypes, CANB!, GH!, K!).

Plantae *Patersoniae lowii* Stapf similes, sed ab ea foliis 3–3.5 mm latis marginibus laevigatis, spathis inaequalibus interna 40–45 mm longa externa 35–40 mm longa, carinis marginibusque spatharum laevigatis, tubo perianthii laevigato atque ovario ca. 12 mm longo distinguuntur.

Tufted perennials 18–35 cm high; stems compressed, ?green, oval in section, 18–35 cm × ca. 1.5 mm, flexed above sheathing part of uppermost leaf and then usually slightly inclined. Leaves ca. 10 per shoot in 2 ranks, basal, mostly slightly exceeding flowering stem; blades 3–5 mm wide, when dry closely striate, surface (30× magnification) smooth or obscurely papillate (*de Wilde & de Wilde-Duyfjes 16390*), margins smooth, rounded, hyaline, uppermost leaf sheathing the lower half (to 2/3) of stem, apex reaching beyond upper 2/3 of stem. Rhipidial spathes orange-brown, unequal, inner 40–45 mm, outer ca. 35–40 mm, spathe keels and margins smooth; floral bracts dry-membranous, margins smooth. Flowers lilac-blue; perianth tube ca. 22 mm, smooth; outer tepals ovate, ca. 12 × 7.5 mm, inner tepals ?lacking; filaments united in a column ca. 1.5 mm; anthers ca. 2 mm; ovary ellipsoid, ca. 12 mm, smooth; style dividing at apex anthers, stigma lobes unknown. Capsules ellipsoid, ca. 20 mm long, smooth; seeds ellipsoid, smooth, glossy dark brown, obscurely striate, ca. 2 × 1 mm; micropylar caruncle white, flattened, ovate, appressed to surface ca. 0.5 mm long. Flowering recorded in January and April.

Discussion. Endemic to the high mountains of northern Sumatra in Indonesia, *Patersonia borneensis* is evidently restricted to high elevations on Gunung (Mt.) Leuser in the Gunung Leuser National Park. Van Steenis, who made the first collection in 1937, noted that he found no trace of the plant on nearby mountains. It can be distinguished from other Malesian species of *Patersonia* by the absence of vestiture or any kind on the leaves, spathes, and floral bracts. Even the perianth tube is completely hairless. In one collection, *de Wilde & de Wilde-Duyfjes 16390*, papillae are visible on the leaf surface at 30× magnification but not as clearly as in *P. borneensis*, the only other Malesian species with minutely papillate leaf surfaces. The general aspect of *P. sumatrensis* most closely approaches that of *P. lowii*, especially in height, but the somewhat narrower leaves usually slightly exceed the stem, which is weakly flexed above the sheathing portion of the uppermost leaf, a feature recalling the otherwise rather different *P. inflexa* of eastern Papua New Guinea.

Paratypes. INDONESIA. **Sumatra:** Gunung Leuser Nature Reserve, W top of Gunung Leuser, 2200–2700 m, 4 Apr. 1975, *W. J. J. de Wilde & B. E. E. de Wilde-Duyfjes 16074* (fr.) (K, L); 13 Apr. 1975, *W. J. J. de Wilde & B. E. E. de Wilde-Duyfjes 16390* (K, L); Mt. Leuser, *Dillon Ripley s.n.* (PH).

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SEQUENCING NEW WORLD ECOSYSTEMS: COMPARISON OF THE CRETACEOUS AND CENOZOIC APPEARANCE OF HABITATS WITH BIOME-CHARACTERIZING PLANT GROUPS[1]

Alan Graham[2]

ABSTRACT

Concepts about development of the plant component of New World terrestrial ecosystems through deep time have reached a point where it is possible to consider some subtle and refining details about the process. One such detail is the temporal relationship between the opportunity of new habitats provided by the physical processes of landscape development and long-term climate change, and the availability of the mostly angiosperm lineages that presently occupy these habitats. Some habitats (e.g., beach/strand/dune) were in existence long before the rise of the flowering plants ca. 125 million years ago (Ma), and some did not develop until late in the Neogene from a combination of cooling climates and locally to regionally increasing elevations (alpine tundra/páramo). In other instances, both habitats and lineages existed contemporaneously, but in different parts of the world, so development of the particular ecosystem had to await the appearance and spread in the New World of the lineage through migration (e.g., *Rhizophora* L. into modern mangrove habitats after the Late Eocene; *Quercus* L. from the north into modern oak–*Weinmannia* L. habitats only after 330 thousand years ago (Kyr). The temporal correspondence between opportunity and availability joins the more widely recognized forcing mechanisms of geologic and climate change, acting on evolutionary processes, as one additional factor in better understanding the origin, composition, and distribution of the ecosystems that presently characterize the New World.

Key words: Ecosystems, environments, Late Mesozoic, lineages, New World, Tertiary.

Sorting the events, processes, and chronologies involved in assembling New World ecosystems has reached a point where broad summaries are forthcoming that serve as a baseline for incorporating new discoveries and fine-tuning existing scenarios. The term "ecosystem" as used here refers to the living envelope or biome, climate, and geological features such as soils and topography that have interacted over time to produce recognizable segments of the Earth's landscape—e.g., tundra, boreal forest, desert, grasslands, deciduous forest, mangroves, and rainforest. Summaries have been compiled for major geographic regions such as North America (e.g., Graham, 1999), the West Indies (Woods & Sergile, 2001), Amazonia (Hoorn & Wesselingh, 2010; Hoorn et al., 2010), and Latin America (Graham, 2010a); others treat specific ecosystems such as tropical montane cloud forests (Churchill et al., 1995; Kappelle & Brown, 2001; Bruijnzeel et al., 2010) and the tropical rainforest (Morley, 2000), while others attempt broader histories for the New World intended for a general audience (Graham, 2010b, 2011). These summaries provide an opportunity to refine details in that history.

Most of the Earth's modern biomes have a prominent angiosperm component so this identifies the Middle to Late Cretaceous as a convenient starting point because after an origin in the Early Cretaceous to possibly the Late Jurassic, flowering plants began to diversify and radiate to become the characteristic element of most present vegetation. The approach here and in other publications by Graham (1999, 2010a, 2010b) has been to 1) identify the principal changes in geology (i.e., physical, topographic histories) and climatic environments that shaped the evolution of ecosystems in the Americas from about the Middle and Late Cretaceous (ca. 100 million years ago [Ma]) to the end of the Pliocene (ca. 2.6 Ma); 2) compile inventories of representative plants for each of the modern ecosystems, indicating which plants were present in the plant fossil record for the region and for this interval (Appendix 1); 3) track the progression of ecosystem development from the appearance of individual elements, through early versions, to essentially modern versions of the

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communities (Graham, 2010b: table 7.1, 2011), and now as an additional refinement; and 4) compare the appearance of habitats with the appearance of lineages available to occupy these habitats that together helped shape the versions of the ecosystems present today.

Geologic and Climatic Environments

In the Cretaceous the initial separation of South America from Africa started in the south at ca. 120 Ma and reached the north coasts of the continents ca. 100–90 Ma. Atmospheric CO_2 concentration in the Maastrichtian was ca. 1000 parts per million by volume (ppmv), probably not exceeding 1300 ppmv, and global mean annual temperatures (MATs) were ca. 11.2°C warmer than at present (Andrews et al., 1995). There were equable maritime climates, high sea levels, extensive epicontinental seas, flooded coastlines, low pole-to-pole thermal and biodiversity gradients with little evidence of significant or sustained glaciers, broad continental connections, and widespread distribution of many plant and animal species. At the Cretaceous/Tertiary boundary ca. 65 Ma, the asteroid impact (Nichols & Johnson, 2008) caused extinction of up to 50% of all species (more among the marine plankton) and altered the reptile (predator)–mammalian (prey) balance and other evolutionary dynamics. There was a slight and temporary lowering of global temperatures from ash that blocked sunlight, followed by rising temperatures from increased CO_2 and other greenhouse gas concentrations (Beerling, 2007) but with no long-term effect on climate (Crowley & North, 1991); and possibly some selection toward deciduousness. In the Middle and Late Cretaceous (ca. 100–70 Ma), the epicontinental seas and coastal waters began to retreat due to the uplift of continents and decreased formation of submerged, water-displacing plateaus. Temperatures cooled by ca. 4°C (Zachos et al., 2008) as CO_2 out-gassing waned from the slowing of plate motion, and South America separated from North America. In the Late Paleocene/Early Eocene (ca. 55 Ma), a sudden increase in atmospheric CO_2 concentration (Sexton et al., 2011) to ca. 1300–1600 pppv occurred, possibly involving emission from explosive vents in the Norwegian Sea as Greenland separated from Europe, and there was a further increase in MAT, perhaps as much as 5°–6°C in the equatorial regions (Head et al., 2009). An early version of the lowland Neotropical rainforest reached its maximum extent from an origin ca. 58–55 Ma (Wing et al., 2009), and tapir, crocodile, and Musaceae (banana-like) lineages extended to within the Arctic Circle. From these peaks in temperature, moisture, and distribution of tropical vegetation, the atmospheric CO_2 concentration declined, ranging from 1000 to 1500 ppmv between 34 and 24 Ma (Middle to Late Eocene; Pagani et al., 2009), and temperatures began an episodic descent from the hothouse interval of the Paleogene into the icehouse times of the Neogene.

Between 49 and 44 Ma (Middle Eocene), spreading along the mid-Atlantic Ridge reached the North Atlantic disrupting the land bridge between North America and Europe at about the same time as temperatures began to cool. During this interval the proto-Greater Antilles emerged as an eastward-moving volcanic island arc that was colliding with the Bahamas Platform. Around 40 Ma the Rocky Mountains and the Andes Mountains were in an early period of uplift, and at 32 Ma South America separated from Antarctica to become an island continent. This initiated the cold Humboldt Current that began cooling the west coast of South America. Continental glaciation began on Antarctica near the Eocene/Oligocene boundary ca. 34 Ma (Bo et al., 2009), and a drop in temperature at the end of the global Middle Miocene Climatic Optimum (MMCO) initiated alternating full-scale glacial and interglacial fluctuations on Antarctica at ca. 17 Ma (Andrill Antarctic Geologic Drilling Project of the sea floor, McMurdo Sound, <http://www.andrill.org>). Between ca. 10 and 6 Ma, the Andes Mountains attained the near-final half of their present maximum height, rising from an average of 2000 to 4000 m (Oncken et al., 2006; Graham, 2009a, 2010a: 88–97, 2010b: 76–88). Around 5–3 Ma there was a Pliocene warm period and although sea levels may have risen by ca. +20 m (<http://www.andrill.org>), uplift and accumulating volcanics in present-day southern Central America reunited South America with North America through formation of the Isthmian Land Bridge at ca. 3.5 Ma. Widespread continental glaciations began in the Quaternary, which was recently defined by the International Commission on Stratigraphy and the International Union for Quaternary Research as beginning 2.6 Ma (see Giles, 2005).

These physical and climatic events acting on evolutionary processes within lineages resulted in a sequence of ecosystems beginning with eight versions recognized for the Cretaceous. These were 1) the polar broad-leaved deciduous forest, 2) notophyllous broad-leaved evergreen forest, 3) paratropical rainforest, 4) tropical forest, 5) aquatic, 6) herbaceous freshwater bog/marsh/swamp, 7) mangrove, and 8) beach/strand/dune. One hundred million years later, events and processes have resulted in the 12 versions

currently recognized for the New World. These are 1) desert, 2) shrubland/chapparal-woodland-savanna, 3) grassland, 4) mangrove, 5) beach/strand/dune, 6) freshwater herbaceous bog/marsh/swamp, 7) aquatic, 8) lowland Neotropical rainforest, 9) lower to upper montane broad-leaved forest (deciduous forest), 10) coniferous forest, 11) alpine tundra (páramo), and 12) tundra. The terminology, composition, proposed developmental sequence, and chronology of this transformation have been discussed earlier (Graham, 1999, 2010a, 2010b, 2011). The inventories on which they are based are included in the tables and appendices of Graham (1999, 2010a), respectively, and representatives are given in Appendix 1.

Inventories

After reviewing the geologic and climatic events contributing to the development of New World ecosystems the next step is to compile the representative plant genera that characterize the 12 modern ones (Graham, 1999, 2010a, cf. references). The last step logically would be to consult an inventory of Cretaceous and Tertiary plants for the region. Ideally, the entries would have been assessed for accuracy of the age, locality, and identification of the specimens, and would include the relevant literature and location of the types. Although compilations of the fossil record for individual genera and families are available (e.g., Juglandaceae, Manos et al., 2007; Rubiaceae, Graham, 2009b; Lythraceae, S. Graham, in prep.), no overall database exists. New discoveries rapidly render printed summaries of plant family histories, phylogeny, and biogeography obsolete even when published only shortly before (e.g, for the Lythraceae, S. Graham, personal communication, 2011). Several electronic and printed versions have been attempted (see Graham, 2010a: xiii) and others are underway, including a catalog of Cretaceous and Cenozoic vascular plants for the New World (<http://www.mobot.org/mobot/research/CatalogFossil/catalog.shtml>; see Graham, 2012, in this issue), but it will be a long time before a dependably complete inventory is available. In the meantime, prominent genera in the plant biome that are part of modern New World ecosystems and their fossil representation (based on Graham, 1999, 2010a: app. 1 and 2, and references cited therein) are presented in Appendix 1. This compilation allows only a shadowy insight into the correspondence between habitat opportunity and the appearance of lineages suitable to occupy those habitats. Experience has shown that it will be tempting to use the partial inventories and new discoveries of fossil plants to prematurely reinvent such concepts as tropical rainforest and environmental dynamics, the history of northern temperate elements in the Latin American biota, leaf/climate relationships, closure of the isthmian land bridge, and refugia. Even so, and even with the limitations of the database in its present state, the records currently allow refinements in the history of the plant component of New World ecosystems. As the inventory improves, a sharper image of this history is emerging.

Ecosystem Development

The sequence of appearance of Cretaceous and Tertiary ecosystems in the New World has been summarized in Graham (2010b: 174–198, 209–228, 235–267, 275–299, table 7.1; 2011). Elements (E in table 7.1) of most ecosystems appeared in the Cretaceous and Paleogene, but they coalesced into early versions (EV) and then into essentially modern versions (EM) in the Cretaceous (e.g., aquatic communities, lower to upper montane broad-leaved forests), Paleogene (coniferous forest, lowland Neotropical rainforest, modern New World mangroves), during and just after the MMCO (widespread grasslands, tropical dry forests, and related vegetation types), and in the Middle Miocene and Pliocene (deserts, lowland tundra, alpine tundra, or páramo). An influencing factor and another detail in this gradational development was the subtle, but nonetheless recognizable, interaction between the appearance of suitable habitats and the appearance of modern lineages to occupy these habits, allowing definition of the present-day ecosystems.

Habitat Opportunities and Lineage Availability

Some lineages defining the plant formations and associations of the New World ecosystems coevolved in concert with the relatively recent appearance of local to regional suitable habitats (e.g., *Lupinus* L., Hughes & Eastwood, 2006; *Polylepis* Ruiz & Pav., Simpson, 1986; the parrot genus *Pionus*, Ribas et al., 2007) in the Andean Highlands. Other progenitors were likely introduced periodically via migration and persisted when and if suitable habitats appeared. The subject of this study is to examine approximately when, for example, did *Betula* L. and *Acer* L./*Quercus* L. and *Juglans* L. (in eastern North America); *Pinus* L. and *Quercus* (Mexico, northern Central America); *Quercus* and *Weinmannia* L. (highlands of Colombia); Poaceae (mid-continent North America, central Argentina); *Rhizophora* L. (tropical and warm-temperate coasts); *Pinus–Picea* A. Dietr.–*Abies* Mill.–*Tsuga*

(Endl.) Carriére–*Alnus* Mill.–*Betula*–*Populus* L.–*Salix* L. (mountains of northwestern North America); *Decodon* J. F. Gmel.–*Cabomba* Aubl.–*Nymphaea* L.–*Pachira* Aubl.–*Trapa* L.–*Typha* L. (various aquatic habitats); and genera that would eventually form the lowland Neotropical rainforest come together to constitute the present-day beech-maple/oak-hickory associations of the deciduous forest formation; the pine-oak association of the mid-altitudes of northern Latin America; the oak–*Weinmannia* woods of the Andean forest belt of Colombia; the grasses of the prairies and pampas; the modern *Rhizophora*-dominated mangrove communities; the coniferous and boreal forests of the high altitudes and latitudes; aquatic communities with a prominent angiosperm component; and the modern rainforest? That is, what was the temporal relationship between the physical opportunity provided by geologic and climatic events (namely, the presence of suitable habitats) and the availability of lineages to occupy those habitats as a development in defining modern New World ecosystems? Aquatic and brackish-water coastal conditions were available long before the Cretaceous; dry to arid seasonal habitats developed extensively during and after the MMCO; and cold, high-altitude environments appeared in the Mio-Pliocene and Quaternary when the later phases of Andean and other mountain uplift combined with cooling trends in the Neogene. However, *Rhizophora* did not appear in the New World until the beginning of the Middle Eocene; many northern temperate deciduous elements, present since the Late Cretaceous and Paleogene in the high latitudes, did not move south in significant numbers to modernize the temperate forests of northern Latin America until the decline in temperature after the MMCO; and although *Quercus* is known from North America since the Late Cretaceous, it did not appear in northern South America until about 330 thousand years ago (Kyr) to form the modern oak–*Weinmannia* community of the upper Andean forest. This study explores the temporal correspondence between habitat opportunity and lineage availability as suggested in Appendix 1, even as it presently stands, as one factor in conceptualizing the sequence of development of modern New World ecosystems.

AQUATIC AND FRESHWATER HERBACEOUS BOG/MARSH/SWAMP

These habitats have been available since the origin of the lithosphere and were ready for colonization by angiosperms whenever they appeared (ca. 125 Ma or before). Aquatic and other freshwater environments were already occupied by a variety of angiosperm families in Early Cretaceous and Paleocene times; hence, they are among the oldest essentially modern (namely, angiosperm-dominant) versions of present-day ecosystems. This is not unexpected given that wetland/aquatic seasonally unpredictable habitats, along with fluctuating dry sites in West Gondwana, are considered places of origin and/or early differentiation of the flowering plants. From Appendix 1 it is seen that Cretaceous and Paleogene lineages available in the New World that took advantage of this habitat opportunity were the Araceae (*Pistia* L.), Cabombaceae (*Brasenites*, extinct), Ceratophyllaceae (*Ceratophyllum* L.), Haloragaceae (*Obispocaulis*, *Tarahumara*, both extinct), Lemnaceae (*Limnobiophyllum* extinct), Lythraceae (*Decodon*, *Trapa*), Nymphaeaceae and plants with nymphaealean affinities (*Aquatifolia*, *Paranymphaea*, *Pluricarpaella*, all extinct), Trapaceae (now part of Lythraceae; *Hemitrapa*, extinct; note that *Trapa* in pre-Miocene North American floras [e.g., Barnett, 1989] may be *Hemitrapa*; the paleocomplex of related/similar genera needs revision; S. Graham, personal communication, 2011), incertae sedis: *Iara* (extinct), *Quereuxia* (extinct, *Trapago*); several probable aquatics from the Lower Cretaceous Crato Formation of Brazil (Mohr & Friis, 2000); in addition to the Azollaceae–*Azolla* Lam. and other older fern and allied groups. The related freshwater herbaceous bog/marsh/swamp habitat was early occupied by *Sphagnum* L., *Selaginella* P. Beauv., *Equisetum* L., and various ferns, but the record of early angiosperms in this environment is not well known.

BEACH/STRAND/DUNE

This is another ancient habitat, but because conditions for preservation are poor in the coarse, shifting sand environment, the history of the ecosystem is not well known. The earliest New World records for the Aizoaceae (a family that includes, e.g., the extant *Sesuvium portulacastrum* (L.) L.), Amaranthaceae (*Iresene* P. Browne), Batidaceae (*Batis maritima* L.), Convolvulaceae (*Ipomoea pes-caprae* (L.) R. Br.), Fabaceae (*Canavalia maritima* Thouars), Poaceae (*Uniola paniculata* L.), Polygonaceae (*Coccoloba uvifera* (L.) L.), and others that can range into the habitat may extend back into the Cretaceous (e.g., Fabaceae) and Paleocene (Poaceae), but fossil records for these genera are unknown or are comparatively recent, probably due, in part, to taphonomy.

LOWER TO UPPER MONTANE BROAD-LEAVED FOREST (LATIN AMERICA)/DECIDUOUS FOREST (EASTERN NORTH AMERICA)

Terrestrial habitats extending from the coast to the moderate Cretaceous and Paleocene highlands were

available in the Cretaceous and were soon occupied after 125 Ma by a version of this ancient ecosystem. It has an extensive representation in the fossil record (Appendix 1). Present in the Cretaceous and Paleocene were Aceraceae (possibly *Acer*; oldest record Late Cretaceous, Hell Creek Formation, South Dakota; see reference to Kirk Johnson's ongoing study noted in Renner et al., 2008), Araucariaceae (*Araucaria* Juss.; extinct organ genera *Araucariopitys*, *Araucarioxylon*, *Araucarites*), Atherospermataceae (Laurales; *Laurelia*, extinct), Betulaceae (*Betula*; oldest record Middle Eocene Allenby Formation, British Columbia, Canada; Crane & Stockey, 1987), Carpinaceae (*Carpinus* L.–*Ostrya* Scop., as pollen), Ebenaceae (*Diospyros* L.), Ericaceae (*Andromeda* L.), Fagaceae (*Nothofagus* Blume, *Quercus*; *Quercinium*, extinct), Fagaceae s.l. (*Antiquacupula*, *Protofagaceae*, both extinct), Ginkgoaceae (*Ginkgo* L.), Hamamelidaceae (*Allonia*, extinct), Lauraceae (*Persea* Mill. type), Magnoliaceae (*Magnolia* L.), Malvaceae (*Javelinoxylon*, extinct), Platanaceae, Podocarpaceae (*Dacrydium* Lamb., *Podocarpus* L'Hér. ex Pers.; *Gamerroites*, *Podocarpidites*, both extinct), Taxaceae (*Acmopyle* Pilg.), Taxodiaceae (*Glyptostrobus* Endl., *Metasequoia* Hu & W. C. Cheng; *Athrotaxites*, *Taxodioxylon*, both extinct), Theaceae (as *Ternstroemites*, extinct, Early Eocene), Tiliaceae, Ulmaceae (*Ulmus* L.); in addition to *Adiantum* L., *Blechnum* L., *Dennstaedtia* Bernh., *Dryopteris* Adans., *Gleichenia* Sm., *Hymenophyllum* Sm., *Thyrsopteris* Kunze, and other older fern and allied groups that can occur in this community.

LOWLAND NEOTROPICAL RAINFOREST

The physical factors supporting this biome are a low-lying elevation generally less than 900 m, high water table, relatively level terrain so slope and exposure do not cause rapid removal of water, and rapid mineral recycling resulting in soils sterile at depth. The climate factors are a high and relatively uniform temperature (MAT ca. 24°C with the coldest-month mean at least 18°C), and high and relatively uniform mean annual precipitation (MAP) of ca. 1500–1800 mm to a maximum of 11,000 mm with the driest four months receiving at least 18% of the annual rainfall; if MAP falls below ca. 1500–1800 mm, the vegetation trends toward dry forest and savanna. The question is when did these physical and climatic factors first develop over an extensive area in the New World to provide the physical opportunity for development of a recognizable lowland Neotropical rainforest?

By ca. 100–90 Ma, northward spreading along the Mid-Atlantic Ridge had reached the vicinity of northwestern Africa–northeastern South America and the two continents began to fully separate (Veblen et al., 2007). This disrupted the vast continental interior of West Gondwana and was followed by marine inundation of the proto-Amazonian lowlands. Deposition of the Late Cretaceous limestone substrate (Wanderley-Filho et al., 2010) constituted much of the floor and defined the initial underlying topography of the basin. Early uplift of the Northern Andes began draining the basin and isolating the Amazon and Solimões sub-basins in the Cretaceous–Paleogene. This was followed by periodic and partial marine inundation of riverine and lacustrine freshwater habitats during the Tertiary with reversal of the Amazon and Orinoco rivers from west into the Pacific to east into the Atlantic in about the Middle Miocene (ca. 15 Ma; Hoorn & Wesselingh, 2010). Thus, the Early Paleogene (ca. 60 Ma) was a suitable time in terms of physical habitat for beginning the development of an extensive lowland Neotropical rainforest in the New World. This was also a time of climatic warmth and moisture that would culminate with the Early Eocene Climatic Optimum (EECL) ca. 55 Ma.

Elements of a rainforest were present in the earliest Paleocene in places like Colorado (64 Ma; Elaeocarpaceae, Lauraceae, Sterculiaceae) and many had a leaf physiognomy typical of tropical species (entire margins, drip tips), but composition-wise this flora also included lineages that presently are primarily temperate like Platanaceae and Tiliaceae (Johnson & Ellis, 2002). The consensus is that an ecosystem representing an early version of rainforest first began assembling over an extensive area in the New World between ca. 58 and 55 Ma (Burnham & Graham, 1999; Burnham & Johnson, 2004; Wing et al., 2009). A lowland Neotropical rainforest was able to take shape because several angiosperm plant groups were adapted or were adapting to tropical conditions and were present to take advantage of the opportunity provided by the geologic and climatic events and trends (Appendix 1). These included Actinidiaceae (*Parasaurauia*, extinct)/Araceae, Arecaceae, Fabaceae, Malvaceae, Menispermaceae, and Zingiberales (Wing et al., 2009); Elaeocarpaceae and Sterculiaceae (Johnson & Ellis, 2002); and Lauraceae (*Mauldinia*, extinct; family level: Johnson & Ellis, 2002; Wing et al., 2009).

CONIFEROUS FOREST

Although gymnosperms were prominent in the pre-Early Cretaceous vegetation and remained intermingled with angiosperms, usually in diminishing numbers and kinds after the flowering plants rose

to dominance (Graham, 2010a: 374), coniferous gymnosperms forming a forested modern ecosystem did not appear until later. The varied factors combining to produce habitats allowing conifers to compete favorably and persist amidst the diversifying and radiating angiosperms are discussed in Graham (1999: 8). The climatic factor included globally cooling temperatures just after the EECL, augmented regionally by the physical factor of increasing elevations. Uplands further resulted in greater moisture stress (physiological aridity) by runoff/evaporation from slope and exposure to which gymnosperms are morphologically and physiologically adapted (sunken stomata, tannin-containing cell vacuoles). A time and place in which the physical factors early combined to make extensive habitats available for the development of a coniferous forest ecosystem was ca. 49–48 Ma in the Northern Rocky Mountains regions as represented by the Republic Flora of northeastern Washington. Here *Abies*, *Chamaecyparis* Spach, *Picea*, *Pinus*, *Pseudolarix* Gordon, *Thuja* L., *Tsuga*, and the oldest definite *Betula* from the Middle Eocene Allenby Formation, British Columbia, Canada (Crane & Stockey, 1987), combined to produce a western montane association of the coniferous forest formation. This association spread into lowlands to form a boreal forest, and in the highlands farther south as an alpine forest just below timberline, beginning with cooling after the EECL and especially in Oligocene and later Neogene times.

The lineages available already in the Late Cretaceous and Paleocene, or that soon coevolved to take advantage of this habitat opportunity (Appendix 1), were *Abies*, *Picea*, *Pinus*, *Tsuga*, possibly "*Acer arcticum*" of the aff. Aceraceae complex, and Betulaceae (*Betula*) from several Late Cretaceous and Paleocene sites (e.g., Graham, 1999: 162, et seq.).

MANGROVE

Coastal and river inlet brackish-water, tropical to warm-temperate habitats are ancient and in the Late Cretaceous through about the Middle Eocene they were occupied by ferns (e.g., spores of cf. *Acrostichum* L., mangrove fern), palms (*Nipa* Thunb.), and a plant of unknown biological affinities producing pollen called *Brevitricolpites* abundant in pre-Middle Eocene tropical low-lying coastal deposits. However, the plant that presently characterizes much of the New World mangrove ecosystem, *Rhizophora*, did not appear until about the beginning of the Late Eocene (Graham, 1995; 2010a: 489–490, and references therein) and this dates the earliest, essentially modern, version of mangrove vegetation in the Americas at ca. 34 Ma.

GRASSLANDS

The presence of extensive grass-dominated ecosystems such as prairie and pampas has had a long attenuated history (Graham, 2010b: 33–37). Physical conditions suitable for the eventual development of grasslands began with the retreat of the epicontinental sea from mid-continent North America in the Middle to Late Cretaceous. This left a limestone substrate weathering into calcareous soil favorable for the growth of grasses. The rise of the Rocky Mountains to heights sufficient to create a rain shadow in the mid-continent region toward the end of the Eocene (possibly earlier locally) was a second factor. This reduced precipitation, but low pressure systems from the Gulf of Mexico provided some moisture, so conditions were too dry for extensive forests but too wet for deserts. As grasses increased in prominence, fire became an increasingly important reinforcing event. Climate was a culminating factor because by the Middle Miocene (ca. 17–13 Ma) cooling had reached a point where reduced evaporation from ocean surfaces created widespread drying and greater seasonality. This was when elements began to increasingly coalesce into early versions of grasslands and communities of dry aspect.

The earliest evidence of grasses are phytoliths from Late Cretaceous coprolites of India (Piperno & Sues, 2005; Prasad et al., 2005), and in the New World from the Early Eocene of Tennessee (Crepet & Feldman, 1991; Graham, 1999: 170, 2010a: 261). The northern grassland as an extensive, recognizable ecosystem comes into its own, however, only about and just after the Mid-Miocene drying with the gradual decrease of forests. The Palouse Prairie to the west of the Rocky Mountains in Oregon developed ca. 3 Ma when the rise of the Cascade Ranges created drying to the lee side. The pampas of Argentina as a distinct, recognizable community developed in response to the rise of the Southern and Central Andes and also to the global trend toward drying and deciduousness in and after the Middle Miocene. It is also located under the descending arm of the Hadley atmospheric circulation cell. These are also factors in the presence of the monte and Gran Chaco located between ca. 20° and 40°S latitude (Graham, 2010a: 42–44).

SHRUBLAND/CHAPARRAL–WOODLAND–SAVANNA AND DESERT

Evidence from geology (increasing slope, exposure, rain shadows, paleosols), and climate (cooling

temperature, increasing dryness, greater seasonality) provides a context for comparing the opportunity provided by increasing dry habitats with the availability of dry-adapted lineages. This evidence supports the intuitive assumption that dry to arid ecosystems would appear at about the same time as grasslands and fully develop somewhat later in the Neogene with increasing dryness (Graham, 1999: 266–268, 2010a: 261–262). Progenitors were present as individual elements and local early versions by the Middle Eocene (e.g., Green River Flora, Colorado/Utah, ca. 45 Ma; *Ephedra* L. throughout the Americas), but soils, landscape, and climate combined to produce extensive, essentially modern versions in the Middle Miocene and especially in Late Miocene and Pliocene. It is also evident from Appendix 1 that fewer genera characterizing distinctly drier vegetation are present in the Cretaceous and Paleocene floras than in the vegetation types previously discussed, and those in the later Paleogene often represent wide-ranging taxa found in other habitats (e.g., *Acacia* Mill., *Aesculus* L., *Ilex* L., *Jacaranda* Juss., *Pinus*, *Quercus*). The families were present, but the genera forming the shrubland/chaparral–woodland–savana mostly came later and coalesced in the Neogene. True deserts become most evident and most extensive in the plant fossil record during the Late Miocene/Pliocene and during the interglacials of the Quaternary.

The concept of a Neogene origin for modern deserts is the contribution primarily of Daniel Axelrod (1950, 1979, 1983). An essential component of that concept is that the rise of the western mountains, particularly the Sierra Nevada, to heights sufficient to create rain shadows to the lee side is a relatively recent event. The assumption is currently being debated and higher elevations earlier in the Cretaceous and Tertiary are being proposed (Dokka & Ross, 1995; Wernicke et al., 1996; Wolfe et al., 1997; House et al., 1998; Poage & Chamberlain, 2002; Retallack et al., 2004; Stock et al., 2004; Mulch et al., 2006; Schuster et al., 2006). This emphasizes the need to conceptualize the development of modern ecosystems as typically gradational and that concept is facilitated by the device of recognizing elements, early versions, and essentially modern versions appearing over time.

TUNDRA AND ALPINE TUNDRA (PÁRAMO)

This is the last physical and climatic environment to appear extensively in the New World. Tundra habitats depended on the culmination of the Neogene cooling trend in the Late Pliocene (5–3 Ma) and in the Quaternary beginning ca. 2.5 Ma, and alpine tundra/páramo, additionally, upon the elevation of highlands toward their maximum altitudes. Asteraceae, Cyperaceae, Ericaceae, Fabaceae, Juncaceae, Poaceae, Rosaceae, and others appeared long before the Neogene, but the physical and climatic conditions were local and late in coming and the lowland and alpine tundra, along with modern deserts, are the most recent of the Earth's ecosystems to appear.

Refining the details of the origin and history of New World ecosystems has become possible only after the broad outlines of geologic, climatic, and biotic events and processes were established (Graham, 1999, 2010a, 2010b, and references therein). In my later summaries culminating this particular series of studies, two such details have been considered: 1) the broad and overlapping sequence of appearance of the ecosystems (Graham, 2011); and 2) the correspondence between the appearance of habitats, and the presence of lineages to occupy these habitats, which further defines the sequence (present paper).

The latter observation adds a nuance to concepts about ecosystem origin and evolution. It capitalizes on the baseline data consisting of identifications, integration with results from other lines of inquiry, and interpretation within the broadest context of ancillary information (namely, a systems approach; Graham, 2010b: 2–5). A guesstimated 95% or more of ecosystem evolution is determined by the forcing mechanisms of geologic events and climatic change acting on evolutionary processes. It is suggested here that a small but significant refinement additionally involves the correspondence between opportunities for colonization provided by physical alterations in the environment and the fortuitous availability of lineages resulting from the random processes of evolution and dispersion.

In compiling this information it became evident that considerably better databasing of the paleobotanical record is needed. In Appendix 1 an asterisk (*) or double-asterisk (**) designates the genus or at least the family is reported in the fossil record. The others are characteristic genera of the ecosystems, and establishing a record for them would be especially useful in further clarifying lineage histories and paleoenvironmental reconstructions. Even in the present state of knowledge, however, it is evident that various habitats were available long before there were angiosperm lineages to occupy them (aquatic, freshwater herbaceous bog/marsh/swamp, beach/strand/dune). At other times the potential lineages or progenitors were present before there were suitable topographic and climatically defined habitats for

them to coalesce and expand (grassland, shrubland/chaparral–woodland–savanna in the Mid-Tertiary; tundra, alpine tundra/páramo in the Late Tertiary and Quaternary). In still other instances both habitats and genera were available but in different parts of the world, and formation of the modern ecosystem had to await migration (e.g., *Rhizophora* into the Americas, and *Quercus* into South America; the invasives of their time). Continuing alpha-level investigations (namely, the discovery of new fossil floras and revision of existing ones), improving geologic and paleoclimatic context, and refinements in the details (Little et al., 2010; Luna-Vega & Magallón, 2010; Manchester & O'Leary, 2010; Martínez-Millán, 2010), including the one discussed here, continue to provide an increasingly clearer picture of the Earth's past and present ecosystems.

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APPENDIX 1. Modern plant genera prominent in New World ecosystems with emphasis on those known from the fossil record. Some genera range through more than one vegetation type or community association (in boldface). Extensive lists of certain taxa (e.g., grasses) are not included because individual genera usually cannot be recognized from fossils (Geisler, 1945). Genera indicated (*) are those reported from the Cretaceous and/or Tertiary of the New World. Similarly, families marked (**) represent where generic identifications of macrofossils are uncertain, or where generic distinction among microfossils is difficult (Cyperaceae, Poaceae, Amaranthaceae–Chenopodiaceae, noted as chenoam, Ericaceae, etc.). A single dagger (†) designates an extinct taxon. References to records include Graham (1999: tables and index, 2010a: app. 2, 2010b, 2011), Dillhoff et al. (2005) (Early–Middle Eocene, British Columbia, Canada), Falcon-Lang and Cantrill (2001, Middle Cretaceous, Antarctica), and Hoffman and Stockey (1999, Late Paleocene, Alberta, Canada). The oldest family records are designated as Cretaceous or Paleocene, e.g., **Haloragaceae, Cretaceous, Mexico. Identifications may include cf. affinities or form-type designations, e.g., *Ambrosia* L. type. For Quaternary records, see Graham (1999, 2010a).

DESERT, SHRUBLAND/CHAPARRAL–WOODLAND–SAVANNA

Many putative taxa (*) come from the Mid- to Late Tertiary and from midden remains of Quaternary age.

NORTH AMERICA (INCLUDING MEXICO)/ANTILLES/CENTRAL AMERICA

Acacia* Mill., *Achyranthes* L. (chenoam), *Acidoton* Sw., *Adenostoma* Hook. & Arn., **Aesculus* L., *Agave* L., **Amelanchier* Medik., **Amorpha* L., **Arctostaphylos* Adans., **Asteraceae (Ambrosia* L./*Franseria* Cav., **Artemisia* L.), **Astronium* Jacq., **Baccharis* L., *Beaucarnea* Lem., *Bejaria* Mutis ex L., **Berberis* L., **Brahea* Mart. ex Endl., *Bromelia* L., *Brosimum* Sw., *Brya* P. Browne, **Bucida* L., **Bursera* Jacq. ex L., *Byrsonima* Rich. ex Kunth, Cactaceae (*Carnegiea* Britton & Rose, *Cephalocereus* Pfeiff., *Cereus* Mill., *Echinocactus* Link & Otto, *Echinocereus* Engelm., *Ferocactus*, *Lemaireocereus* Britton & Rose, *Mammillaria* Haw., *Myrtillocactus* Console, *Neobuxbaumia* Backeb., *Opuntia* Mill., *Pachycereus* (A. Berger) Britton & Rose, **Pereskia* Mill.), **Caesalpinia* L., **Calliandra* Benth., **Capparis* L., **Cardiospermum* L., **Casearia* Jacq., **Cassia* L., **Ceanothus* L., **Cedrela* P. Browne, **Celtis* L., **Cercidium* Tul., **Cercocarpus* Kunth, **chenoam (*Amaranthus* L., *Atriplex* L., *Chenopodium* L., *Suaeda* Forssk. ex J. F. Gmel.), *Chrysobalanus* L., *Chrysothamnus* Nutt., **Coccoloba* P. Browne, **Comocladia* P. Browne, **Condalia* Cav., **Copaifera* L., *Coulterella* Vasey & Rose, **Crataegus* L., **Crescentia* L., **Croton* L., **Cupania* L., *Curatella* Loefl., *Cyrtocarpa* Kunth, **Dalbergia* L. f., **Dalea* L., **Daphnopsis* Mart., *Dasylirion* Zucc., *Encelia* Adans., **Enterolobium* Mart., **Ephedra* L., **Ericaceae (**Arbutus* L., **Arctostaphylos*), *Erythea* S. Watson, **Erythroxylum* P. Browne, *Eugenia* L. (microfossils as **Eugenia/Myrcia* DC., with other genera of the family having similar pollen; Graham, 1980), **Euphorbia* L., *Flourensia* DC., **Fouquieria* Kunth, **Guettarda* L., *Haematoxylum* L., **Haplorhus* Engl., *Hechtia* Klotzsch, **Holodiscus* (K. Koch) Maxim., **Hymenaea* L., *Idria* Kellogg, **Ilex* L., *Ipomoea* L., **Iresine* P. Browne, **Jacaranda* Juss. (widespread), **Jatropha* L., *Juliania* La Llave & Lex., **Juniperus* L., *Kalmia* L., **Karwinskia* Zucc., *Koeberlinia* Zucc., *Lachnocaulon* Kunth, **Laetia* Loefl. ex L., **Larrea* Cav., *Leucophyllum* Humb. & Bonpl., **Lithocarpus* Blume, **Lysiloma* Benth., **Mahonia* Nutt., cf. **Malpighia* L., *Microcycas* (Miq.) A. DC., **Mimosa* L., *Nolina* Michx., *Olneya* A. Gray, *Parkinsonia* L., *Parthenium* L., **Persea* Mill., **Phyllanthus* L., *Pictetia* DC., *Pieris* D. Don., **Pinus* L., **Piscidia* L., **Pithecellobium* Mart., *Platymiscium* Vogel, ***Poaceae*, **Prosopis* L., **Pseudosmodingium* Engl., **Psychotria* L., *Purshia* DC. ex Poir., **Quercus* L., **Rauwolffa* Cothen, **Rhamnus* L., **Rhus* L., *Rondeletia* L., *Roseodendron* Miranda, possibly **Salicornia* L. (as *chenoam), *Salvia* L., **Sapindus* L., **Sapium* Jacq., **Sarcobatus* Nees, **Sophora* L., **Tabebuia* Gomes ex DC., *Tabernaemontana* L., **Tetragastris* Gaertn., cf. **Tillandsia* L., **Tiquilia* Pers., *Vitex* L., *Yucca* L., **Zamia* L., **Zanthoxylum* L. **Gallery/riparian forests:** **Populus* L., **Salix* L.

SOUTH AMERICA

Including cerrado/caatinga, Patagonian steppe; some overlap with drier phases of the lower to upper montane broad-leaved forest: **Acacia*, **Acnistus* Schott, *Agave*, **Aspidosperma* Mart. & Zucc., **Asteraceae (Mutisioideae–Carduoideae affinities, Middle Eocene, 47.5 Ma, northwest Patagonia, Barreda et al., 2010), possibly *Atriplex* (as **chenoam), **Attalea* Kunth, *Barnadesia* Mutis ex L. f.,

Bejaria, **Berberis*, *Bolax* Comm. ex Juss., *Bonnetia* Mart., *Bowdichia* Kunth, *Bromelia*, **Brosimum*, *Bulnesia* Gay, **Bursera*, **Byrsonima*, Cactaceae (*Armatocereus* Backeb., **Cereus*, **Opuntia*, *Oreocereus* (A. Berger) Riccob., **Pereskia*, *Trichocereus* (A. Berger) Riccob.), **Caesalpinia*, *Cantua* Juss. ex Lam., **Capparis*, *Casearia*, **Castela* Turpin, *Castilla* Cerv, **Cavanillesia* Ruiz & Pav., **Cedrela*, **Ceiba* Mill., *Centrolobium* Mart. ex Benth., *Cercidium*, **Chlorophyllum* Liais, *Chrysobalanus* (family **Chrysobalanaceae, Pliocene), *Chuquiraga* Juss., *Clusia* L., *Colliguaja* Molina, *Copaifera*, *Copernicia* Mart. ex Endl., **Cordia* L., **Croton*, **Curatella*, **Cyperaceae (*Bulbostylis* Kunth, *Hypolytrum* Pers., *Scleria* P. J. Bergius), **Didymopanax* Decne. & Planch., **Dodonaea* Mill., **Drimys* J. R. Forst. & G. Forst., *Duranta* L., *Empetrum* L., **Enterolobium*, **Ephedra*, *Eriotheca* Schott & Endl., **Erythrina* L., *Euphrona* Vell., *Fabiana* Ruiz & Pav., *Gallesia* Casar., *Geoffraea* L., **Guaiacum* L., **Guarea* F. Allam. ex L., **Gunnera* L., *Hesperomeles* Lindl., *Hypericum* L., **Hyptis* Jacq., *Junellia* Moldenke, **Kielmeyera* Mart. ex Zucc., *Lampayo* F. Phil. ex Murillo, **Larrea*, *Lippia* L., **Lomatia* R. Br., **Loxopterygium* Hook. f., **Machaerium* Pers., **Maximiliana* Mart. (type, Pliocene), *Maytenus* Molina, **Mimosa*, *Monvillea* Britton & Rose, *Nassauvia* Comm. ex Juss., *Oreocallis* R. Br., **Ouratea* Aubl., *Palicourea* Aubl., *Pernettya* Gaudich., **Phyllanthus*, *Phytelephas* Ruiz & Pav., *Platymiscium*, **Poaceae (*Axonopus* P. Beauv., *Spartina* Schreb., *Trachypogon* Nees), *Poulsenia* Eggers, **Pouteria* Aubl., *Pradosia* Liais, **Prosopis*, **Pseudobombax* Dugand, **Rauwolffa*, **Roupala* Aubl., *Samanea* (Benth.) Merr., **Schinopsis* Engl., **Senecio* L. (widespread), **Smilax* L., **Spondias* L., **Stillingia* L., **Tabebuia*, *Thibaudia* Ruiz & Pav. ex J. St.-Hil., **Tillandsia*, *Vallesia* Ruiz & Pav., **Vantanea* Aubl., **Vochysia* Aubl., *Welwitschiaceae (Cretaceous, Brazil), **Zanthoxylum*, **Ziziphus* Mill.

Gallery/Riparian Forests (e.g., through the Gran Chaco)

Arecastrum (Drude) Becc., *Albizia* Durazz., *Banara* Aubl., *Croton*, **Enterolobium*, **Ficus* L., *Geoffroea* Jacq., *Hexachlamys* O. Berg, *Holocalyx* Micheli, **Inga* Mill., **Nectandra* Rol. ex Rottb., *Patagonula* L., **Peltophorum* (Vogel) Benth., *Peschiera* A. DC., *Phytolacca* L., **Pisonia* L., **Ruprechtia* C. A. Mey., *Sorocea* A. St.-Hil., **Trichilia* P. Browne; **riparian widespread:** **Salix*, **Schinus* L.; **monte:** **Acacia*, *Atamisquea* Miers ex Hook. & Arn., **Caesalpinia*, **Celtis*, *Cercidium* (e.g., Quaternary, Mexico), *Condalia*, **Larrea*, **Mimosa*, *Prosopis* (e.g., Quaternary, Mexico), **Ziziphus*.

Grassland

**Poaceae; *Pariana* Aubl. (no annulus around pore on pollen), some phytoliths, and **Zea* L. (large size of pollen) identifiable to *genus, others only to **family.

Mangrove

Acrostichum* L., **Avicennia* L., *Conocarpus* L., *Hibiscus* L. (pollen identifiable as **Hampea* Schltdl.–*Hibiscus*), **Laguncularia* C. F. Gaertn., **Nypa* Steck (as †Spinozonocolpites*; extinct in the New World after the Eocene), **Pelliceria* Planch. & Triana (southern Central America, northern South America; not presently known from Mexico or the Antilles), **Pterocarpus* Jacq. (e.g., Plio-Pleistocene, El Salvador), **Rhizophora* L.

South America

Genera above and **Crenea* Aubl. and **Pelliceria* Planch. & Triana.

Beach/Strand/Dune

Achyranthes, *Batis* P. Browne, *Bontia* L., **Bucida* L., *Byrsonima*, Cactaceae (*Melocactus* Link & Otto, *Pilocereus* Lem.–*Cephalocereus*), *Canavalia* Adans., *Catesbaea* L., possibly *Suaeda* (as **chenoam), *Chrysobalanus*, *Cnidoscolus* Pohl, **Coccoloba*, *Colubrina* Rich. ex Brongn., **Comocladia*, **Cordia*, **Dodonaea* Mill., *Erithalis* P. Browne, *Ernodea* Sw., **Euphorbia*, **Guettarda*, *Gymnanthes* Sw., *Heliotropium* L., **Hibiscus* (microfossils as **Hampea* Schltdl.–*Hibiscus*), *Hippomane* L., *Ipomoea*, **Iresene* (chenoam, pollen of genus recognizable), *Jacquinia* L., *Lantana* L., **Manilkara* Adans., **Metopium* P. Browne, *Pectis* L., *Phyllanthus*, *Phyllostylon* Capan. ex Benth. & Hook. f., **Poaceae (*Cenchrus* L., *Uniola* L.), *Portulaca* L., *Rachicallis* DC., *Randia* L., **Reynosia* Griseb., *Scaevola* L., *Sesuvium* L., *Suriana* L., *Thespesia* Sol. ex Corrêa; **primarily present in other habitats but extending into the beach/strand/dune community:** **Acacia*, **Caesalpinia*, **Caesearia*, **Capparis*, **Coccoloba*, **Dalbergia* L. f., **Drepanocarpus* G. Mey., *Eugenia* (pollen identifiable as **Eugenia/Myrcia*, with other genera of the family having similar pollen), **Iresine*, **Laguncularia*, *Malache* B. Vogel, *Piscidia*, *Terminalia* L. (pollen identifiable as **Combretum* Loefl./**Terminalia*), **Tournefortia* L., *Ximenia* L.

Freshwater Herbaceous Bog/Marsh/Swamp

This includes the pantanal. Some taxa are facultative aquatics, growing rooted in standing water. Some shrubs/trees may range into the swamp, but fully wooded swamps (**Nyssa* L., **Taxodium* Rich., **Tillandsia*; Asian **Glyptostrobus* Endl. as fossil in the New World) are included as a low, wet phase in the lower to upper montane broad-leaved forests.

Acoelorraphe* H. Wendl., *Ascyrum* L., **Bravaisia* DC., *Calathea* G. Mey., **Coccoloba*, *Coccothrinax* Sarg., **Cyperaceae (Carex* L., e.g., seeds, Pliocene, Alaska; *Cladium*, *Cyperus* L., *Eleocharis* R. Br., *Rhynchospora* Vahl, *Scirpus* L.), **Drosera* L., **Equisetum* L. (e.g., Cretaceous, Alaska; Alberta, Canada; Late Paleocene, Alberta, Canada), **Fraxinus* L., *Gerardia* Benth., **Heliconia* L., **Isoetes* L. (Late Paleocene, Alberta, Canada), Juncaceae (**Juncus* L.), *Lobelia* L., **Poaceae (*Paspalum* L., *Phragmites* Adans.), **Polygonum* L., **Sabal* Adans., **Sagittaria* L., **Sphagnum* L., **Typha* L., *Valisneria* Scop., **Vicia* L.

Aquatic

Many putative taxa (*) occur in the Cretaceous and Paleocene; see, e.g., **Haloragaceae.

Azolla* Lam. (Cretacous, Argentina; Paleocene, Alberta, Canada, Hoffman & Stockey, 1999), *Brasenia* Schreb., **Cabomba* Aubl., **Cabombaceae (*†*Brasenites*, Cretaceous, Kansas, Wang & Dilcher, 2006), **Ceratophyllum* L. (Cretaceous, Mexico, Estrada-Ruiz et al., 2009), **Ceratopteris* Brongn., **Cyperaceae (*Eleocharis*), **Decodon* J. F. Gmel. (Cretaceous, Mexico, Estrada-Ruiz et al., 2009), *Eichhornia* Kunth, **Haloragaceae (as *†*Obispocaulis*, *†*Tarahumara*; Cretaceous, Mexico), **Hygrophila* R. Br., *†*Iara* (family unknown, Cretaceous, Argentina, Fanton et al., 2006), *Lemna* L., **Lemnaceae/Araceae (*†*Limnobiophyllum*, Paleocene, Alberta, Canada, Stockey et al., 1997; Hoffman & Stockey,

1999), *Limnocharis* Bonpl., **Ludwigia* L., **Myriophyllum* L., *Najas* L., **Nelumbo* Adans., **Nuphar* Sm., **Nymphaea* L., **Nymphaeaceae (*†*Aquatifolia*, Cretaceous, Kansas, Wang & Dilcher, 2006), *†*Nymphoides* Ség., **Pachira* Aubl., *†*Paranymphaea* (fossil, Paleocene, Argentina; Saskatchewan, Canada), **Pistia* L. (Paleocene, Saskatchewan, Canada), *†*Pluricarpellatia* (nymphaealean, Cretaceous, Brazil, Mohr et al., 2008), **Poaceae (e.g., species of *Luziola* Juss., *Paspalum* L., floating mats, South America), **Polygonum*, *Pontederia* L., **Potamogeton* L., **Sagittaria*, **Salvinia* Ség., **Thalia* L., **Trapa* L. (Eocene, U.S.A., anything earlier probably belongs to *†Hemitrapa*, S. Graham, personal comm., 2011), *†*Trapago* (syn. *†*Quereuxia*, affinity unknown, Cretaceous, Alberta, Canada, Stockey & Rothwell, 1997; S. Graham, personal comm., 2011), **Utricularia* L., *Vallisnera* Cothen., *Victoria* Lindl. (South America); **salt-water marshes:** possibly *Salicornia*, *Suaeda* (as **chenoams).

Lowland Neotropical Rainforest

Several (**) are known from the Paleocene, where generic identifications of macrofossils are uncertain or where generic distinction among microfossils is difficult.

TROPICAL ELEMENTS PRESENTLY EXTENDING INTO THE UNITED STATES

**Avicennia* L., *Conocarpus*, **Laguncularia* C. F. Gaertn., **Palmae, **Rhizophora* L.

Atanikerdluk flora

This Paleocene flora was documented from Greenland by Boyd (1990, 1992).

*†*Musophyllum* (now *†*Musopsis*, Heliconiaceae–Musaceae–Strelitziaceae complex).

Castle Rock flora

This flora dates to 64.1 Ma, Colorado (Johnson & Ellis, 2002).

*Elaeocarpaceae, *Lauraceae, *Sterculiaceae.

NORTH AMERICA (CANADA, UNITED STATES, MEXICO)/ ANTILLES/CENTRAL AMERICA

**Actinidiaceae (*†*Parasaurauia*, Late Cretaceous, Georgia, Herendeen et al., 1999), **Aegiphila* Jacq., cf. **Aguiaria* Ducke, **Alchornea* Sw., **Allophylus* L., *Anthodiscus* G. Mey., *†*Antrophyllum*, **Arecaceae, cf. **Astrocaryum* G. Mey., *Batocarpus* H. Karst., **Bernoullia* Oliv., **Bombacaceae, **Brosimum* Sw., *Calophyllum* L., **Campnosperma* Thwaites, *Caryocar* L., **Cavanillesia* Ruiz & Pav., **Cedrela*, **Ceiba*, cf. **Chamaedorea* Willd., *Chaunochiton* Benth., **Chomelia* Jacq., cf. **Cionosicyos* Griseb., **Combretum–Terminalia*, *Couratari* Aubl., **Crudia* Schreb., **Ctenitis* (C. Chr.) C. Chr., *Dialium* L., *Elaeis* Jacq., **Faramea* Aubl., **Ficus*, **Guarea*, **Gustavia* L., cf. **Hiraea* Jacq., *Huberodendron* Ducke, **Lauraceae (*†*Marmarthia*, Late Cretaceous/Late Maastrichtian Hell Creek Formation, North Dakota, South Dakota, Montana, Johnson, 1996; *†*Mauldinia*, Late Cretaceous, Georgia, Herendeen et al., 1999), **Lycopodium* L., **Matayba* Aubl., **Meliosma* Blume (Late Paleocene, Alberta, Canada, Hoffman & Stockey, 1999), *Minquartia* Aubl., **Ophioglossum* L., **Paragonia* Miers ex Bureau, *Parkia* R. Br., cf. **Paullinia* L., *Peltogyne* Vogel, **Poaceae, *Poulsenia*, *Prioria* Griseb., cf. **Protium* Burm. f., **Pseudolmedia* Trecul., **Pteris* L., **Sapium*, **Selaginella* P. Beauv., **Spathiphyllum* Schott, **Sphaeropteris* Bernh.–*Trichipteris* C. Presl, *Swietenia* Jacq., **Symphonia* L. f., cf. **Tetrorchidium* Poepp., *Uribea* Dugand & Romero, **Vantanea*.

SOUTH AMERICA

There is an extensive record; see references in Graham (2010b).

Cerrejón flora

This flora dates to 58 Ma in Colombia (Wing et al., 2009).

Akania* Hook. f. (presently eastern Australia; Paleocene, Argentina), **Anacardium* L., **Anthurium* Schott, **Apeiba* Aubl., **Araceae, **Arecaceae, **Asplundia* Harling, **Asteraceae, **Astrocaryum* G. Mey., **Blechnum* L. type, **Bombax* L., **Brownea* Jacq., **Callitriche* L., *Carapa* Aubl., **Carex*, **Casuarina* L., cf. **Catopsis* Griseb., *Catostemma* Benth., **Cecropia* Loefl., **Cedrela*, **Ceiba*, **Cochlospermum* Kunth, **Combretum–Terminalia*, *cf. *Connarus* L., **Cordia*, **Coussapoa* Aubl., **Crescentia* L., **Crudia*, **Cyclanthus* Poit. ex A. Rich., **Ecclinusa* Mart., **Elatine* L., **Eleocharis*, **Erythrina*, *Eschweilera* Mart. ex DC., *Euterpe* Mart., cf. **Evodianthus* Oerst., **Fabaceae, **Ficus*, *Geonoma* Willd., **Gunnera*, **Heliconia*, **Humiriastrum* (Urb.) Cuatrec., **Hymenophyllum* Sm., **Ilex*, **Inga*, *Iryanthera* (A. DC.) Warb., **Jamesonia* Hook. & Grev., **Juncus*, **Lacmellea* H. Karst., **Lauraceae, *Licania* Aubl., **Lomariopsis* Fée, **Lophosoria* C. Presl., **Lycopodium*, **Lygodium* Sw., **Machaerium*, **Macoubea* Aubl., **Macrolobium* Schreb., **Malvaceae, **Manicaria* Gaertn., *Mauritia* L. f., **Menispermaceae, *Montrichardia* Crueg., **Ochroma* Sw., **Pachira* Aubl., **Parinari* Aubl., *Parkia* R. Br., *Pentaclethra* Benth., **Peumus* Molina, ***Poaceae*, cf. **Polygonum*, **Psittacanthus* Mart., **Pteris*, **Pterocarpus*, *Scheelea* H. Karst., **Schinopsis*, **Selaginella*, **Swartzia* Schreb., **Symphonia*, **Tabebuia*, *Vatairea* Aubl., **Vochysia*, *Warszewiczia* Klotzsch; **várzea: **Alchornea*, **Anacardium*, **Astrocaryum*, *Calophyllum*, *Carapa*, *Cedrelinga* Ducke, **Ceiba*, **Cordia*, **Crudia*, *Euterpe*, **Ficus*, **Guarea*, **Hernandia* L., *Hura* L., **Luehea* Willd., **Macrolobium* Schreb., **Manicaria*, *Maquira* Aubl., **Mauritia* L. f., **Ocotea* Aubl., *Oenocarpus* Mart., *Phytelephas*, **Pithecellobium*, *Platymiscium*, **Poaceae (e.g., **Echinochloa* P. Beauv.), **Pseudobombax*, *Raphia* P. Beauv., **Rheedia* L., **Sapium*, cf. **Scirpus*, **Selaginella*, **Socratea* H. Karst., **Sphagnum* L., **Sterculia* L., **Thoracocarpus* Harling, *Triplarina* Raf., *Vatairea* Aubl., **Virola*, *Warszewiczia*, *Xylopia* L., **Xyris* L.; **Atlantic forest:** *Arapatiella* Rizzini & A. Mattos, *Buchenavia* Eichler, **Dicksonia* L'Hér., **Podocarpus* Labill.; **also cultivated and/or harvested:** **Araucaria* Juss., **Astronium*, **Caesalpinia*, **Cedrela*, **Dalbergia*, *Dialium*, *Diploon* Cronquist, **Drimys*, **Ecclinusa*, *Eriotheca*, *Eschweilera*, *Hevea* Aubl., **Ilex*, *Licania*, **Luehea*, **Manilkara*, **Nectandra*, **Ocotea*, **Paullinia*, *Plathymenia* Benth., *Simira* Aubl., *Sprucella* Stephani, *Theobroma* L., **Virola*.

Lower to Upper Montane Broad-leaved Forest

In Latin America, this includes cloud forests, elfin forests, ceja, and some gymnosperm/conifer enclaves; many putative identifications for genera and families (*, **) are Late Cretaceous and Paleocene.

**Acer* L., **Adiantum* L. (Cretaceous, Argentina), **Aetanthus* (Eichler) Engl., **Alfaroa* Standl.–*Oreomunnea* Oerst.,

*Alchornea, *Allophylus, *Alnus Mill., *Alsophila R. Br., *Araucaria (Cretaceous, Mexico), **Arecaceae, **Asteraceae, *Astrocaryum, *cf. Banisteriopsis C. B. Rob., *Bauhinia L., Befaria Mutis ex L., *Bernardia Houst. ex Mill., *Blechnum (Cretaceous, Argentina), *Bombax, *Brunellia Ruiz & Pav., *Bucida, *Bursera, *Caesarea Cambess., Calophyllum, Carapa, *Carpinus L., *Catostemma Benth., *Cavanillesia Ruiz & Pav., *Cecropia (secondary, widespread), *Cedrela, *Ceiba, Ceratozamia Brongn., *Chamaedorea, Charianthus D. Don., **chenoam (*Iresine), Chlorophyllum, *Chrysophyllum L., *Clethra L., *Cleyera Thunb., *Clusia L., *Coccoloba, *Cordia, *Cornus L., *Cosmibuena Ruiz & Pav., *Cupania, *Cupressus L., *Cyathea Sm., *Cymbopetalum Benth., *Cyrilla Garden ex L., *Dacrydium Lamb. (Cretaceous, Argentina), Dacryodes Vahl–*Sloanea L. (low-altitude wet forests, Antilles), *Danaea Sm., *Daphnopsis, *Dendropanax Decne. & Planch., *Dennstaedtia Bernh. (Cretaceous, Argentina), *Desmanthus Willd., *Dichapetalum Thouars, Didymopanax, *Dioscorea L. type, *Diospyros L., cf. *Doliocarpus Rol., *Drimys, *Dryopteris Adans. (Cretaceous, Argentina), **Ericaceae (*Cavendishia Lindl. type), *Erythrina L. (widespread), *Eucommia Oliv. (extinct in the New World), Eugenia (as *Eugenia–Myrcia), Euterpe, **Fagaceae (*†Quercinium, Cretaceous, Mexico), **Fagaceae s.l. (*† Antiquacupula, *†Protofagacea, Cretaceous, Georgia, Herendeen et al., 1999), *Fagus L., *Faramea, *Ficus (widespread), Freziera Willd., Gaussia H. Wendl., *Gleichenia Sm. (Cretaceous, Argentina), cf. *Glycydendron Ducke, *Grammitis Sw., *Guarea, *Guazuma Mill., *Gustavia L., **Hamamelidaceae (*†Allonia, Cretaceous, Georgia, Herendeen et al., 1999), *Hampea/Hibiscus, *Hauya DC., *Hedyosmum Sw., *Heliconia, *Hemitelia R. Br.–Cnemidaria C. Presl, *Hiraea, *Hymenaea, *Hymenophyllum (Cretaceous, Argentina), *Ilex, *Jacaranda, *Jamesonia/Eriosorus Fée complex, **Juglandaceae (as *†Monopites fossil pollen, referrable to Alfaroa, Engelhardia Lesch. ex Blume, Oreomunnea type), *Juglans L., *Justicia L., *Lacmellea, *Laetia, **Lauraceae (*Persea type, Cretaceous, Mexico), *Laurelia Juss. (Cretaceous, Argentina), *Liquidambar L., *Lisianthus L., *Lomariopsis–Stenochlaena J. Sm., *Lonchocarpus Kunth, *Lophosoria, *Luehea, *Lycopodium, *Lygodium, *Magnolia L., *Malpighia L., **Malvaceae (as *†Javelinoxylon, Cretaceous, Mexico), *Manicaria type, *Marcgravia L., Mastichodendron (Engl.) H. J. Lam, *Matayba, **Melastomataceae, *Meliosma, *Mimosa, *Mortoniodendron Standl. & Steyerm., *Myrcia, *Myrica L., *Norantea Aubl., *Ocotea, *Oreopanax Decne. & Planch., Ormosia Jacks., *Ostrya Scop., *Paullinia, *Peltophorum, *Peperomia Ruiz & Pav., Perrottetia Kunth, *Persea, *Petrea L., *Pinus, *Pityrogramma Link, **Platanaceae (Early Paleocene Castle Rock flora), *Platanus L., *Pleodendron Tiegh., **Poaceae, **Podocarpaceae–Taxodiaceae affinities (Cretaceous, Mexico), *Podocarpus (Cretaceous, Argentina), *Populus, *Posoqueria Aubl., cf. *Pouteria, Prestonia R. Br., *Protium, *Prunus L., *Pseudobombax, *Psidium L., *Psilotum Sw., *Psychotria, *Pteridium Gled. ex Scop., *Pteris, *Quercus L., *Rajania L., *Rauwolfia Ruiz & Pav., *Rhamnus, Richeria Vahl, *Roupala Aubl., *Rourea Aubl., Roystonea O. F. Cook, *Rubus L., *Sabicea Aubl., *Salix, Samanea (Benth.) Merr., *Sambucus L., *Sapium, Scheelea, *Securidaca L., *Selaginella, *Serjania Mill., *Smilax, Spathelia L., *Spathiphyllum, *Sphaeropteris/Trichipteris, *Stillingia, *Struthanthus Mart., Styrax L., *Symphonia, *Symplocos, *Synechanthus H. Wendl. type, *Tapirira Aubl., *Tecoma Juss., Terminalia (as *Combretum–Terminalia), *Ternstroemia Mutis ex L. f. (as *†Ternstroemites, Early Eocene, North Dakota, U.S.A.), *Tetragastris, *Tetrorchidium Poepp., *Thyrsopteris Kunze (Cretaceous, Argentina), *Ticodendron Gómez-Laur. & L. D. Gómez (as *†Ferrignocarpum), *Tilia L., **Tiliaceae (Early Paleocene Castle Rock flora), cf. *Tillandsia, *Tontelea Miers., *Tournefortia, *Trithrinax Mart., *Ulmus L., *Weinmannia L., *Zanthoxylum; **open, secondary, clearings:** *Alibertia A. Rich. ex DC., *Borreria G. Mey., *Byttneria Loefl., *Cuphea P. Browne, *Desmanthus, *Dicranopteris Bernh., *Passiflora L., **Poaceae, *Rajania L., *Smilax L.

SOUTH AMERICA/ANTARCTICA

This includes tropical elements extending into the Andean forest belts; many (*, **) identifications are Late Cretaceous and Paleocene.

*Acalypha L., *Acmopyle Pilg. (Cretaceous, Argentina, Chile), *Adiantum, *Alchornea, *Alnus, *Alsophila, *Anemia Sw., *Athyrium Roth, *Antrophyum Kaulf., *Araucaria, **Araucariaceae (Cretaceous, Antarctica; *Araucaria, *†Araucarites, foliage, Falcon-Lang & Cantrill, 2001; *†Araucarioxylon, *†Araucaripitys, wood), *Asplenium L., **Asteraceae, *Austrocedrus Florin & Boutelje, *Blechnum, Bocconia L., Bolax, Bonnetia, *Botrychium Sw., *Bravaisia, Brocchinia Schult. f., Brunellia, *Calophyllum, *Cedrela, *Chrysophyllum, *Clethra, *Clusia, *Cnemidaria–Hemitelia, *Ctenis, *Dacrydium, *Dennstaedtia, *Dicksonia, *Dicranopteris Bernh., *Drimys, *Dryopsis Holttum & P. J. Edwards, Empetrum, Escallonia Mutis ex L. f., Euterpe, *Ficus, *Fitzroya Hook. f. ex Lindl., *Gleichenia, *Guettarda, *Gunnera, Gyranthera Pittier, Hedyosmum, Heliamphora Benth., *Heliconia, Heliocarpus L., *Ilex, **Isoetaceae, *Isoetes, *Juglans, Laplacea Kunth, *Lecythis Loefl., *Libocedrus Endl., *Lippia, *Lonchocarpus, *Maytenus, *Meliosma, *Miconia Ruiz & Pav., Mora Benth., Murraya J. König ex L., *Myrica, *Nephrolepis Schott, *Nothofagus Blume (Cretaceous, Argentina), *Ocotea, *Oreopanax, *Osmunda L., Palicourea, *†Pecopteris Brogn., Pernettya, *Persea, **Poaceae, *Podocarpus (Cretaceous, Argentina, as *†Podocarpidites, *†Gamerroites), *Polystichum Roth, *Protium, *Prunus, *Psychotria, *Pterocarpus, *Rhus, *Sacoglottis Mart., *Salix, *Sambucus, *Saurauia Willd., Sloanea, Stegolepis Klotzsch ex Körn, *Styrax, *Symplocos, *Tabebuia, Talauma Juss., **Taxodiaceae (Middle Cretaceous, Antarctica, *†Athrotaxites, foliage, Falcon-Lang & Cantrill, 2001; *†Taxodioxylon, wood), *Tibouchina Aubl., *Toxicodendron Mill., *Trema Lour., *Trigonobalanus Forman, *Turpinia Vent., Tyleria Gleason, *Urtica L., *Vaccinium L., *Vantanea, *Viburnum L., *Weinmannia, *Zamia.

DECIDUOUS FOREST

This refers to plant communities in eastern North America, mixed with riparian and coniferous forest in western North America.

*Acer (fruits, Cretaceous, Kirk Johnson locality, Hell Creek Formation, South Dakota, see Renner et al., 2008: 798), cf. *†Acer arcticum (Late Paleocene, Alberta, Canada, Sapindaceae, Hoffman & Stockey, 1999), *†Alismaphyllites (Late Paleocene, Alberta, Canada, **Alismataceae, Hoffman & Stockey, 1999), *Alnus Mill. (Dillhoff et al., 2005), *†Amersinia (Late Paleocene, Alberta, Canada, **Cornaceae, Hoffman & Stockey, 1999), *Andromeda L. (e.g., Cretaceous, Greenland), Asimina Adans., **Asteraceae, *†Averrhoites (Late Paleocene, Alberta, Canada, extinct, **Oxalidaceae, Hoffman & Stockey, 1999), *†Beringiaphyllum (Late Paleocene, Alberta, Canada, **Cornaceae, Hoffman & Stockey, 1999), *Betula L. (Dillhoff et al., 2005), *Carpinus–Ostrya (Dillhoff et al., 2005, pollen),

Carya Nutt. (putative, Dillhoff et al., 2005), *Castanea* Mill., *Chaetoptelea* Liebm. (Late Paleocene, Alberta, Canada, Hoffman & Stockey, 1999), *Chamaecyparis* Spach, *Cornus*, *Dennstaedtia* (Late Paleocene, Alberta, Canada, Hoffman & Stockey, 1999), *†*Deviacer* (Late Paleocene, Alberta, Canada, **Sapindaceae, Hoffman & Stockey, 1999), *Diospyros* L. (Cretaceous, Greenland), *Fagus*, *Fraxinus*, *Ginkgo* L. (Cretaceous, Alberta, Canada; Late Paleocene, Alberta, Canada, Hoffman & Stockey, 1999), *Gleditsia* L., *Glyptostrobus* (Cretaceous, Alberta, Canada; Late Paleocene, Alberta, Canada, Hoffman & Stockey, 1999), *Ilex*, *†*Joffrea* (Late Paleocene, Alberta, Canada, related to modern *Cercidiphyllum* Siebold & Zucc., Hoffman & Stockey, 1999), *Juglans* (Dillhoff et al., 2005), *Larix* Mill., cf. *†*Lemnospermum* (Late Paleocene, Alberta, Canada, **Araceae), *Lindera* Thunb., *Liquidambar*, *Liriodendron* L, *†*Macginicarpa* (Late Paleocene, Alberta, Canada, **Platanaceae, Hoffman & Stockey, 1999), *Magnolia* (Cretaceous, Greenland), *Metasequoia* Hu & W. C. Cheng (Cretaceous, Alberta, Canada; Late Paleocene, Alberta, Canada, Hoffman & Stockey, 1999), *Nyssa*, *Osmunda* (Upper Cretaceous; Late Paleocene, Alberta, Canada, Hoffman & Stockey, 1999), *Pinus*, **Platanaceae (*†*Erlinghorfia*, *†*Platanites*, Johnson, 1996, Late Cretaceous/Late Maastrichtian Hell Creek Formation, North Dakota, South Dakota, Montana), *†*Platananthus* (Late Paleocene, Alberta, Canada, **Platanaceae, Hoffman & Stockey, 1999), *Platanus* (Late Paleocene, Alberta, Canada, Hoffman & Stockey, 1999), **Poaceae, *Populus*, *Pterocarya* Kunth (Dillhoff et al., 2005), *Quercus* (Dillhoff et al., 2005), *Salix*, *Taxodium*, *Tilia*, *Ulmus* (Early Middle Eocene, British Columbia, Canada, Dillhoff et al., 2005), *†*Zingiberopsis* (Late Paleocene, Alberta, Canada, Zingiberaceae, Hoffman & Stockey, 1999).

NORTHERN TEMPERATE ELEMENTS IN MID-ALTITUDE EASTERN MEXICO

Abies Mill., *Acer*, *Alnus*, *Carpinus*, *Cornus*, *Diospyros*, *Fagus*, *Ilex*, *Juglans*, *Liquidambar*, *Lycopodium*, *Magnolia*, *Myrica*, *Ostrya*, *Pinus*, *Platanus*, *Populus*, *Prunus*, *Pteridium*, *Quercus*, *Rubus*, *Salix*, *Sambucus*, *Smilax*, *Ulmus*.

WARM-TEMPERATE ELEMENTS WITH NORTHERN TEMPERATE ELEMENTS IN MID-ALTITUDE EASTERN MEXICO

Alfaroa (as *Alfaroa–Oreomunnea*), *Clethra*, *Cyathea*, *Drimys*, *Eugenia* (pollen as *Eugenia–Myrcia*), *Hedyosmum*, *Heliconia*, *Meliosma*, *Peperomia*, *Persea*, *Podocarpus*, *Weinmannia*.

Coniferous Forest

BOREAL CONIFEROUS FOREST

Abies, *Alnus*, *Betula* (family Betulaceae and genus from several sites in northern North America; see Graham, 1999: 162–233; oldest records are from Middle Eocene Allenby Formation, British Columbia, Canada; Crane & Stockey, 1987), *Larix*, *Picea* A. Dietr., *Pinus*, *Populus*, *Salix*, *Sphagnum*, *Thuja* L., *Tsuga* (Endl.) Carriére.

WESTERN MONTANE/ALPINE CONIFEROUS FOREST

Many putative identifications (*, **) have come together for the first time in the Middle Eocene of northwestern North America.

Abies (Dillhoff et al., 2005), *Acer*, *Alsophila*, *Aphanactis* Wedd., **Asteraceae, *Berberis*, *Buddleja* L., *Castanopsis* (D. Don) Spach, *Catopsis*, *Ceanothus*, *Cercocarpus*, *Chamaecyparis*, *Cornus*, *Crataegus*, *Cupressus*, *Cyathea*, *Drimys*, **Ericaceae (*Arbutus*, *Arctostaphylos*, *Menziesia* Sm., *Pernettya*, *Rhododendron* L.), *Garrya* Douglas ex Lindl., *Holodiscus*, *Juniperus*, *Libocedrus*, *Mahonia*, *Myrcia* (pollen as *Eugenia–Myrcia*), *Oreopanax*, *Oxylobus* (DC.) Moc. ex A. Gray, *Picea* (modern distribution to the mountains of northern Mexico; fossils to Veracruz, Mexico, and Guatemala in the Neogene, Dillhoff et al., 2005), *Pinus* (Dillhoff et al., 2005), **Poaceae, *Podocarpus*, *Prunus*, *Pseudotsuga* Carriére, *Quercus*, *Ribes* L., *Sequoia* Endl., *Smilax*, *Tsuga* (Dillhoff et al., 2005); **moist/riparian:** *Alnus*, *Betula*, *Clethra*, *Cornus*, *Fraxinus*, *Ilex*, *Juglans*, *Oreopanax*, *Phoradendron* Nutt., *Platanus*, *Polypodium* L., *Populus*, *Prunus*, *Psittacanthus* Mart., *Salix*, *Struthanthus*, *Styrax*, *Symplocos*, *Tillandsia*, *Umbellularia* (Nees) Nutt., *Xylosma* G. Forst.; **highlands:** *Artemisia* (lower elevations), *Calocedrus* Kurz/*Libocedrus*, *Cupressus*, **Cyperaceae, **Ericaceae (*Gaultheria* L., *Kalmia*, *Rhododendron*, *Vaccinium*), *Erigeron* L., *Picea*, *Pinus*, **Poaceae, *Prunus*, *Pseudotsuga*, *Sequoiadendron* J. Buchholz, *Sphagnum* (upper elevations), *Taxus* L., *Thuja*, *Tsuga*.

APPALACHIAN CONIFEROUS FOREST

Abies, *Betula*, **Ericaceae (*Rhododendron*), *Picea*, *Pinus*.

GULF COASTAL (PINE) CONIFEROUS FOREST

Pinus.

PINE-OAK (MEXICO) CONIFEROUS FOREST

Alnus, *Cuphea*, *Juglans*, *Pinus*, *Populus*, *Quercus*, *Struthanthus*.

Alpine Tundra/Páramo

Many putative taxa (*) are from the Pliocene and Quaternary.

NORTH AMERICA/ANTILLES/CENTRAL AMERICA

Arenaria L., **Asteraceae, *Cerastium* L., *Cirsium* Mill., *Draba* L., *Eryngium* L., *Gnaphalium* L., **Juncaceae (*Luzula* DC.), *Lupinus* L., *Oxylobus*, *Phacelia* Juss., *Plantago* L. (e.g., Late Pliocene, Alaska), **Poaceae, *Potentilla* L., *Puya* Molina, *Ranunculus* L. (Quaternary records, and in the Pliocene of Colombia), *Senecio* (possibly among some pollen identified as *Asteraceae/Compositae).

SOUTH AMERICA (INCLUDING SHRUBBY PLANTS OF THE PUNA)

Acaena Mutis ex L., *Arenaria*, **Asteraceae, *Azorella* Lam., *Baccharis*, *Buddleja*, *Calceolaria* L., **Cyperaceae, *Distichia* Nees & Meyen., *Draba* (North America), *Escallonia*, *Espeletia* Mutis ex Bonpl., *Fuchsia* L., *Gaultheria* L., *Gentiana* L., *Gynoxys* Cass., *Hedyosmum*, *Hypericum*, *Jamesonia*, *Lupinus*, *Miconia*, *Montia* L., *Plantago*, **Poaceae (*Aciachne* Benth., *Calamagrostis* Adans., *Chusquea* Kunth [including *Swallenochloa* McClure], *Deyeuxia*

Clarion ex P. Beauv., *Festuca* L., *Jarava* Ruiz & Pav., *Stipa* L.), **Polylepis* Ruiz & Pav., *Puya*, **Rhizocephalum* Wedd., *Senecio*, **Weinmannia*.

TUNDRA

Many reports (*) are from the Pliocene and Quaternary.

NORTH AMERICA

Isolated clusters of **Abies* and **Picea*, dwarf **Alnus*–**Betula*–**Salix*, **Asteraceae, **Cyperaceae (**Carex*, *Eriophorum* L., *Luzula*), *Dryas* L., *Empetrum*, **Ericaceae (**Arctostaphylos*, *Cassiope* D. Don, *Ledum* L., **Loiseleuria* Desv./*Rhododendron*, **Vaccinium*), **Hippuris* L., *Menyanthes* L., **Poaceae, **Potentilla*, **Rubus*, *Saxifraga* L., *Silene* L.

CATALOG AND LITERATURE GUIDE FOR CRETACEOUS AND CENOZOIC VASCULAR PLANTS OF THE NEW WORLD[1]

Alan Graham[2]

There is need for a source of information in electronic form on fossil plants for purposes of systematics, biogeography, paleobotany, and paleoecology. The principal impediment to such projects has been experience with past efforts that proved too complex to sustain given the resources available (e.g., The International Organization of Palaeobotany's [IOP] Plant Fossil Record, <http://www/uk-bap.org.uk>, later <http://www.paleobotany.org>; Boulter et al., 1991, Holmes, 1991). A number of new electronic catalogs are coming online that deal with subsets of the broader information field such as the holdings of an institution focused on particular geographic regions (the Paleobotany Project of the Denver Museum of Nature and Science; <http://paleobotanyproject.org>), woods (<http://insidewood.lib.ncsu.edu>), pollen and spores (PalDat, the palynological database (<http://www.paldat.org>), or Cenozoic angiosperms (the developing Cenozoic Angiosperm Database within the Paleobiology Database, <http://www.paleodb.org>). The latter will attempt to compile fossil records for all organisms, for all time, and for all places. Numerous other institutions are placing images of fossil specimens online, and the National Science Foundation is encouraging these efforts in the United States through the program for Advancing Digitization of Biological Collections (ADBC). It is clear that until these mega projects are sufficiently well advanced to provide relatively complete records, there is need for subsets of data with different emphasis that can be consulted.

The catalog announced here (<http://www/mobot.org/mobot/research/CatalogFossil/catalog.shtml>) focuses on the plant fossil record as a guide to information on evolution and co-evolutionary processes, calibrating phylogenies, detecting biogeographic patterns, and reconstructing paleoenvironments. It includes the name of the fossil and its family assignment according to the Angiosperm Phylogeny Group (2009) classification, or if a form name is used, the biological affinities as cited by the author (if no affinity is cited at least to the level of family, the record is not included). In addition, the plant part or evidence on which the identification was made (including biochemical fossils and spectral patterns if derivation is cited to genus or family), age, locality, literature reference, and remarks are listed.

Traditional nonelectronic sources currently exist, and although mostly out-of-date, they can be consulted as an initial guide to early reports and literature until other catalogs become more complete. These are Andrews (1970; with supplements by Blazer, 1975, and Watt, 1982), LaMotte (1952), Muller (1981), Archangelsky et al. (2000, et seq.), Germeraad et al. (1968), and Graham (1973, 1979, 1982, 1986, 1999, 2010: app. 1, 2).

Examples from the catalog are presented below for the ferns, gymnosperms, and angiosperms.

Filicineae

†*Conatiopteris schumanii* (Cyatheaceae): Lower Cretaceous (Aptian), upper Chickabally Member, Budden Canyon Formation, near Cottonwood, California, U.S.A., trunk, frond bases, adventitious roots; Lantz et al., 1999: 361: [Cladistic analyses "indicate that the new genus is nested among a paraphyletic assemblage of dicksoniaceous, lophorosiaceous, and metaxylaceous species that subtend a monophyletic Cyathaceae s.s."]

†*Kuylisporites* (†*K. mirabilis*, †*K. separatus*, †*K. scutatus*, †*K. waterbolkii*; Cyatheaceae): Cretaceous, Cenozoic, widespread, spores; Mohr & Lazarus, 1994: 765: ["... genus originated in the Northern Hemisphere in the late Cretaceous; *K. waterbolkii* ... closely related to or identical with extant *Cnemidaria*."]

Gymnospermae

Chamaecyparis Spach sp. (Cupressaceae): Middle Eocene, Thunder Mountain flora, central ID, vegetative axes; Erwin & Schorn, 2005: 125: ["Radiometrically dated at 46–45 Ma, it represents one of the

[1] Visit the catalog at <http://www/mobot.org/mobot/research/CatalogFossil/catalog.shtml>.

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oldest montane conifer-dominated assemblages recovered from the Northern Hemisphere."]

Podocarpus L'Hér ex Pers. (Podocarpaceae): Eocene, western Tennessee, leafy shoots; Dilcher, 1969. *Podocarpus matudae* Lundell: (modern, as a possible pre-Quaternary relict), two plastid DNA markers suggest that a divergence time between the unique haplotypes from a Guatemalan population and the two most common haplotypes from the Sierra Madre Oriental in Mexico was between 10 and 20 Ma, and further haplotype divergence in the poorly resolved clade of the Sierra Madre Oriental occurred between 3 and 0.5 Ma; findings support a Miocene age for temperate floristic elements in Mesoamericana cloud forest, whereas further haplotype divergence within the Sierra Madre Oriental, Chiapas, and Guatemala occurred more recently, coinciding with Pleistocene cloud forest refugia (Ornelas et al., 2010).

ANGIOSPERMAE

Acer L. (Aceraceae): Based on up to seven chloroplast loci, "the nine North American species of *Acer* diverged from their nearest relatives at widely different times; eastern American *Acer* diverged in the Oligocene and Late Miocene; western American species in the Late Eocene and Mid Miocene; and the *Acer* core clade, including *A. saccharum*, dates to the Miocene" (Renner et al., 2008: 795). "The oldest described *Acer* fossils are Paleocene fruits from North America and Eurasia (Wolfe & Tanai, 1987; Crane et al., 1990; Manchester, 1999; Kittle et al., 2005), but still older fruits from the Maastrichtian (66.5 Ma) Hell Creek formation in South Dakota also conform morphologically to *Acer* (K. R. Johnson, pers. comm. to Renner, August 2008). "None of these ancient isolated fruits, however, can securely be assigned to an extant clade" (Renner et al., 2008: 798).

Guatteria Ruiz & Pav. (Annonaceae): Erkens et al. (2007: 399) infer four plastid regions (*matK*, *rbcL*, *trnL-trnF*, *psaA-trnH*) and "three major biogeographical events in the history of the genus: (1) a transoceanic Miocene migration from Central into South America before the closing of the Isthmus of Panama; (2) a major diversification of the lineage within South America; and (3) several migrations of South American lineages back into Central America via the closed Panamanian land bridge. Therefore, *Guatteria* is not an Amazonian centered-genus sensu Gentry but a major Miocene diversification that followed its dispersal into South America." The authors noted (p. 404) that there are no known fossils of the genus, but in addition to *Guatteria*-like phytoliths reported from the Quaternary of Central America, macrofossils (†*G. culebrensis*) are reported from the Miocene of Panama and Peru (unverified; for additional reports of Annonaceae and for references, see Graham, 2010: app. 2.2, 588).

New versions will be placed online about every six months, and additions and corrections are invited.

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REINSTATEMENT AND EXPANSION OF THE GENUS *PERISTETHIUM* (LORANTHACEAE)[1]

Job Kuijt[2]

ABSTRACT

The genus *Peristethium* Tiegh. (Loranthaceae) is re-established to comprise five species previously placed in *Struthanthus* Mart. (*P. aequatoris* (Kuijt) Kuijt, *P. leptostachyum* (Kunth) Tiegh., *P. lojae* (Kuijt) Kuijt, *P. polystachyum* (Ruiz & Pav.) Kuijt, and the new nomenclatural combination presented here, *P. tortistylum* (Kuijt) Kuijt). Also included are five species from *Cladocolea* Tiegh. (*P. archeri* (A. C. Sm.) Kuijt, *P. peruviense* (Kuijt) Kuijt, and *P. primarium* (Kuijt) Kuijt), with two transferred as new nomenclatural combinations herein, *P. nitidum* (Kuijt) Kuijt and *P. roraimense* (Steyerm.) Kuijt). Additionally, five new species are described and illustrated (*P. attenuatum* Kuijt, *P. colombianum* Kuijt, *P. confertiflorum* Kuijt, *P. lamprophyllum* Kuijt, and *P. palandense* Kuijt). The genus *Peristethium* thus consists of 15 species and a key is provided for the genus. It is characterized by pairs of conspicuous, often caducous, chaffy scale leaves at the base of the mostly determinate inflorescences, and by lateral inflorescence units that are triads and/or ebracteolate single flowers called monads (in one case, partly pentads). Some species have bisexual flowers while others are dioecious; flowers are either tetramerous or hexamerous, and one pentamerous species is included (*P. nitidum*). The minute anthers are sessile or nearly so, placed far above the middle of the petals. Geographically, the genus reaches from northern Bolivia to Costa Rica, with two rare, narrow endemics on Mt. Roraima in Venezuela and the Pakaraima Mountains.

Key words: *Cladocolea*, IUCN Red List, Neotropical Loranthaceae, *Peristethium*, *Struthanthus*.

The genus *Struthanthus* Mart. (Loranthaceae) was initially established for a number of South American species (Martius, 1830). The protologue describes the inflorescence as a spike or raceme of paired triads, the flowers being stated as bisexual and the anthers dorsifixed on slender filaments. However, Eichler (1868) would correct Martius's diagnosis by pointing out that *Struthanthus* species are dioecious, the aborted organs of the opposite sex present in both unisexual flower types. Eichler referred to nine Mesoamerican species Martius had not known and added 10 new species for South America in *Flora Brasiliensis*. Numerous further species have been described in the meantime from various Neotropical regions. *Struthanthus* has not been monographed—only local treatments have been published—and the total number of species is thus not precisely known. In 1895, Van Tieghem maintained the genus *Spirostylis* C. Presl ex Schult. & Schult. f. segregated earlier from *Struthanthus* by Presl (in Schultes & Schultes f., 1829), and would add two segregate genera, *Eichlerina* Tiegh. and *Peristethium* Tiegh. These three segregate genera have not been recognized by subsequent workers, except for *Peristethium* as a monotypic genus in Engler and Krause (1935). *Struthanthus* as a whole ranges from northwestern Mexico to Bolivia and Argentina, being absent from the Caribbean.

It has been noted for some time that *Struthanthus* is a paraphyletic assemblage (Kuijt, 1975b). My morphological study of inflorescences in the family suggested that at least three separate intergeneric bridges seemed to exist between the genus and *Cladocolea* Tiegh. (Kuijt, 1981b: 9–12). Each of these bridges consisted of at least two bridgehead species (see Kuijt, 1975b: 279–281). One intermediate species was placed in *Struthanthus*, the other in *Cladocolea*, suggesting that at least part of *Struthanthus* was derived from *Cladocolea*-like ancestors. The most prominent of these bridging intermediaries involved at least *S. leptostachyus* (Kunth) G. Don and *C. archeri* (A. C. Sm.) Kuijt. Other related species discovered since that time seemed to reinforce the bridge concept of species with intermediate morphologies. Recent study, nevertheless, especially of the new species to be described herein, has led to a fundamental reevaluation of the intergeneric connection. From these new insights it

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is herewith proposed to realign the species involved in the *C. archeri–S. leptostachyus* intergeneric bridge as a separate genus, for which the name *Peristethium* is available. This includes the assignment of several species to *Peristethium* thus far resident in *Struthanthus* (*S. aequatoris* Kuijt, *S. leptostachyus*, *S. polystachyus* (Ruiz & Pav.) G. Don, and *S. tortistylus* Kuijt) or in *Cladocolea* (*C. archeri*, *C. nitida* Kuijt, *C. peruviensis* Kuijt, *C. primaria* Kuijt, and *C. roraimensis* (Steyerm.) Kuijt). Additionally, five newly discovered species from Andean South America are herein described and illustrated. As now constituted by these 15 species, the genus *Peristethium* demonstrates coherent, structural, and geographic integrity. Several features, seen in individual species, are unique or nearly so in New World Loranthaceae, even in the family generally, and include an inflorescence most often terminated by a single flower that is preceded by at least one pair of lateral 1-flowered units called monads, an inflorescence bearing a number of basal pairs of papery (often caducous or partially caducous) scale leaves, and extremely small, mostly sessile and basifixed anthers that are positioned near the tips of the subtending petals. The combination of these features is unique in Loranthaceae. *Peristethium* includes both dioecious species as well as some with bisexual flowers; unusual in Neotropical Loranthaceae, some species are tetramerous and others hexamerous.

In retrospect, it can be seen that *Peristethium* as a natural assemblage has been glimpsed in the past without being properly appreciated. The protologue of *Struthanthus tortistylus* Kuijt suggested an affinity to *P. leptostachyum* (Kunth) Tiegh. and *P. polystachyum* (Ruiz & Pav.) Kuijt, these species then still being placed in *Struthanthus* (as *S. leptostachyus* and *S. polystachyus*; Kuijt, 2003a). A study of foliar sclerenchyma pointed in the same direction, suggesting taxonomic connections between *P. archeri* (A. C. Sm.) Kuijt, *P. leptostachyum*, and the two new nomenclatural combinations presented here, *P. primarium* (Kuijt) Kuijt and *P. roraimense* (Steyerm.) Kuijt (as *Cladocolea primaria* and *C. roraimensis*; Kuijt & Lye, 2005). Parallel statements are to be found in the protologue of *C. primaria* (Kuijt, 1987a). The present treatment resolves such ambiguities.

Van Tieghem's protologue of *Peristethium* (Van Tieghem, 1895) is exceedingly sparse and based on the original *Loranthus leptostachyus* Kunth alone. He repeated Martius's error by describing the flowers as bisexual, even though this had been corrected by Eichler (1868). The new genus was founded primarily on the several pairs of partly persistent, chaffy bracts that envelop the young inflorescence, but Van Tieghem, without providing any details, also stated that the stamens are of one type; in reality, they are always placed at two somewhat different heights. Van Tieghem's errors (as applied to the only species then recognized) were repeated by Engler and Krause (1935), who added a further one, namely the threadlike shape of the filaments, all of which are said to be of equal length. As indicated in the generic diagnosis below, bisexual flowers are characteristic of at least one species not known to the above authors, and anthers are sessile or nearly so, threadlike filaments not being present.

The rationale for recognizing *Peristethium* as a segregate from *Struthanthus* and as here circumscribed is based on several structural characters. The most prominent among these is the above-mentioned development of several to many pairs of conspicuous chaffy scale leaves at the base and along the inflorescence axis, the axial ones (bracts) subtending triads and monad. Most of the scales along the fertile axis tend to be caducous, but basal scale leaves often persist. No species of *Struthanthus* possess such scale leaves, but several other, unrelated Neotropical Loranthaceae show similar but much smaller and mostly deciduous scale leaves along the lower inflorescence axes, as in *Panamanthus* Kuijt. In the Old World, a similar, independent evolution of modified scalelike leaves below the flowers has occurred, as in *Diplatia* Tiegh., *Tolypanthus* (Blume) Blume, and several other genera (Kuijt, 1981b). However, the scale leaves in these Old World genera are much larger, often brightly colored, and not deciduous. The above-mentioned scale leaves are to be distinguished from the more inconspicuous pairs of prophylls at the base of axillary ramifications of some mistletoes, e.g., *Psittacanthus mayanus* Standl. & Steyerm. and *P. sonorae* (S. Watson) Kuijt (Kuijt, 2009).

A second important generic character in *Peristethium* is the occurrence in each inflorescence of a single morphologically terminal flower, commonly flanked by one or more pairs of ebracteolate monads. The inflorescence is thus determinate. Paucity of materials has prevented me from confirming this aspect in some species accepted here for *Peristethium*. In at least one unrelated species, *Struthanthus deppeanus* (Schltdl. & Cham.) G. Don in Mexico, the same determinate pattern exists (Kuijt, 1981b), but elsewhere in small-flowered genera in the Loranthaceae this is known only in *Cladocolea*.

A third important generic feature in *Peristethium* is the sessile or nearly sessile, exceedingly small

anther, inserted well above the middle of the petal that bears it. *Struthanthus* characteristically has larger, versatile anthers on long, slender filaments. The other small-flowered genera in the Loranthaceae possess entirely different androecia, especially *Dendropemon* (Blume) Rchb. (Kuijt, 2011a) and many species of the genus *Passovia* H. Karst.; the latter have minute anthers, but can scarcely be held as related to *Peristethium*. The small size of the anthers, and the prominent sterile anthers in male plants, for example, of *P. leptostachyum*, can be problematic in the determination of sex, as shown by the errors made by Van Tieghem (1895) and Engler (1897) in referring to that species as having bisexual flowers. Nevertheless, species with bisexual flowers as well as dioecious species exist in *Peristethium*. Further, the slender shape of the seedling in *Peristethium*, lacking a swollen haustorial pole, has also emerged as a contrasting feature vis-à-vis most other small-flowered genera. Finally, the existence of foliar sclerenchyma is a common denominator for those species that have been investigated (Kuijt & Lye, 2005). The profusion of stellate foliar sclereids is especially remarkable in *P. roraimense*, where much of the leaf mesophyll consists of such cells.

The variation in inflorescence structure seen in *Peristethium* is in general agreement with the evolutionary trends previously outlined for the Loranthaceae (Kuijt, 1981b). In that study, I concluded that the evolution of their inflorescences led from monads to aggregation as triads, and that this process begins at the base of the inflorescence. This latter tendency corresponds to the change from plants with bisexual flowers to a dioecious condition, and that hexamery was derived from tetramery. With regard to triadization, we may see all stages in the process represented in extant species of *Peristethium*. For example, *P. archeri*, *P. peruviense* (Kuijt) Kuijt, and *P. roraimense* have strictly monadic inflorescences. In *P. primarium*, *P. palandense* Kuijt, and several others, triads are present basally while monads are found subterminally and variably. Finally, *P. confertiflorum* may have only triads, with the additional, unanticipated production of some pentads. With the exception of *P. primarium*, all tetramerous species also exclusively have monadic inflorescences, thus combining two putatively ancestral conditions.

The curiously contorted style described and illustrated for *Peristethium polystachyum* and *P. tortistylum* Kuijt (Kuijt) has equivalents in several other Neotropical genera. The majority of Mesoamerican species of *Cladocolea* show this feature, seen more strongly in the female flower than the male (Kuijt, 1975b). In Mexico, it is also known in *Struthanthus*; in fact, the generic synonym *Spirostylis* was based on this stylar twisting in what is now known as *S. interruptus* (Kunth) G. Don (Kuijt, 1975a). *Struthanthus tortistylus* from Ecuador (2003a) was published before it was realized that contorted styles are also characteristic of female *P. polystachyum*, a fact not previously mentioned in the literature. One further species with strongly contorted styles, an as yet undescribed species of *Struthanthus* from Peru, has recently been discovered. Thus we can be assured that there are at least three instances in which this curious, unexplained feature has evolved independently in Neotropical, small-flowered genera. The phenomenon is not known from other Loranthaceae in either the New or Old Worlds, with the solitary exception of *Ileostylus micranthus* (Hook. f.) Tiegh. of New Zealand (Barlow, 1966). The biological significance of contorted styles is not known, but it may bear a relation to the extraordinary behavior of the embryo sac known from Loranthaceae generally (see Kuijt, 1969, for a summary).

As now constituted, *Peristethium* also has convincing geographical integrity: its species range from Amazonian Bolivia north through the Andes into Costa Rica, with two endemic, highly localized outliers on Mt. Roraima and the Pakaraima Mountains (Fig. 1). It is generally accepted that the upper regions of the tepuis of Venezuela and Guyana environmentally correspond to the páramo life zone of the northern Andes (Berry et al., 1995), and the existence of the two rare species, *P. roraimense* and *P. nitidum* (Kuijt) Kuijt, in the Mt. Roraima area is not unexpected. The phylogenetic affinities of *Peristethium* with other small-flowered genera in the Loranthaceae are at present unclear, although the coherence of Psittacanthinae, which also includes the large-flowered genera *Aetanthus* (Eichler) Engl. and *Psittacanthus* Mart., has received molecular affirmation (Vidal-Russell & Nickrent, 2008; Nickrent et al., 2010). However, the precise relationships among the various genera remain to be elucidated. Morphological information, especially the occurrence of tetramerous flowers, determinate inflorescences, and monads lacking bracteoles, at present suggests an affinity of *Peristethium* with *Cladocolea*.

Taxonomic Treatment

Peristethium Tiegh., Bull. Soc. Bot. France 42: 175. 1895. TYPE: *Peristethium leptostachyum* (Kunth) Tiegh. [≡ *Loranthus leptostachyus* Kunth, Nov. Gen. Sp. [H.B.K.] (quarto ed.) 3: 440. 1818 (1820)].

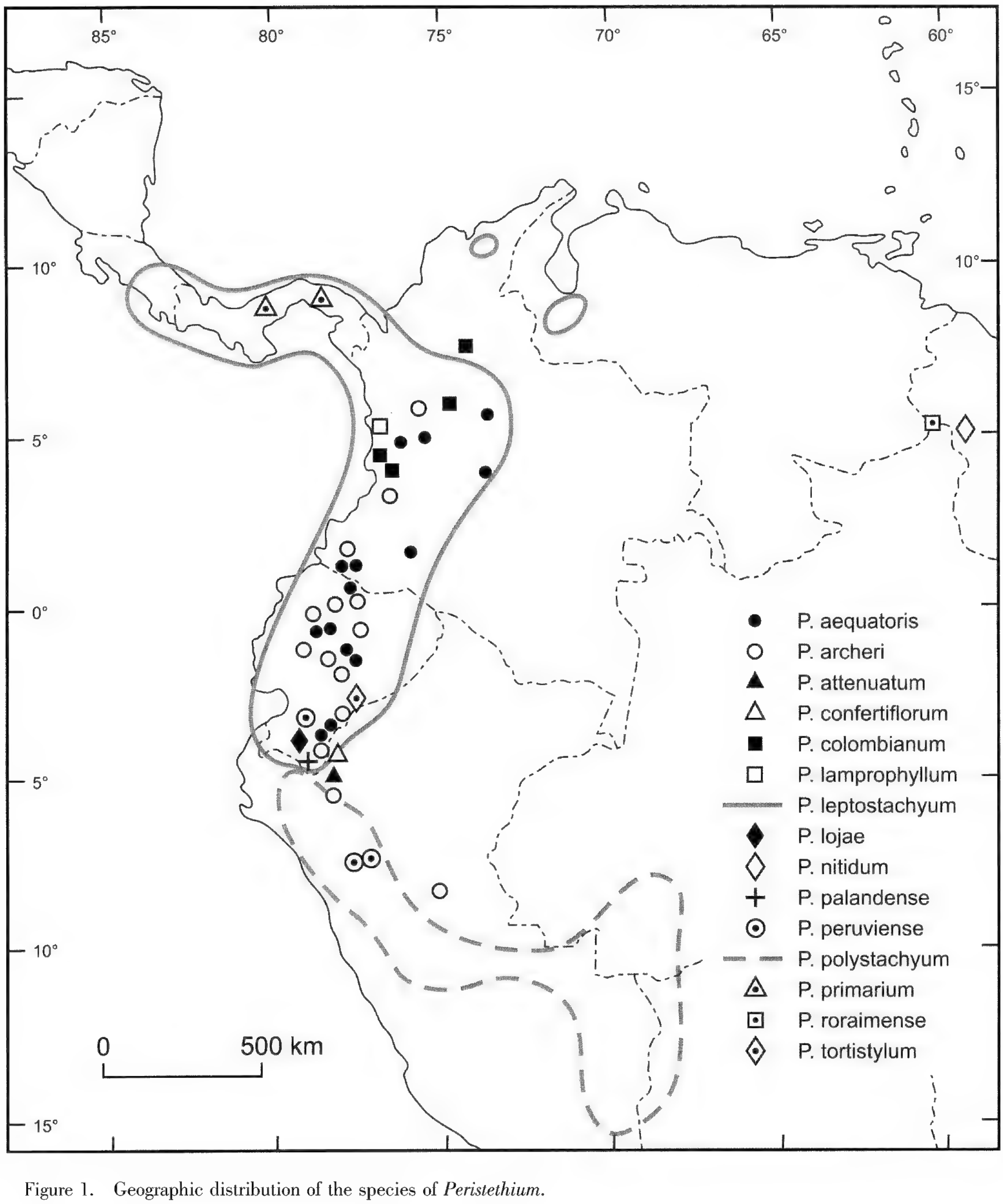

Figure 1. Geographic distribution of the species of *Peristethium*.

Struthanthus Mart., p.p., Flora 13: 102–106. 1830. TYPE: *Struthanthus syringifolius* (Mart.) Mart. [≡ *Loranthus syringifolius* Mart.].

Plants sparsely branched, unisexual when dioecious or bisexual, percurrent (monopodial), rarely determinate; internodes terete to quadrangular, smooth or with numerous rounded lenticels; epicortical roots present on some branches (and at the base of the plant) at least in *Peristhemium aequatoris* (Kuijt) Kuijt, *P. archeri*, *P. leptostachyum*, and *P. lojae* (Kuijt) Kuijt. Leaves paired, ovate to elliptical, apex mostly acute to acuminate; petiolate. Inflorescences in units as monads or triads or mixed (as in the new species presented here, *P. confertiflorum*, with some pentads), the uppermost inflorescence section mostly with monads and terminating in a single flower, the monads ebracteolate; basal inflorescence bracts large, yellowish, chaffy or thick (as in *P. primarium*), bracts caducous where subtending

flowers, variably persistent or caducous at the base; monads, triads, and pentads (when present) pedunculate or more commonly sessile. Flowers tetramerous or hexamerous (*P. nitidum* the only pentamerous exception); anthers minute, ± isomorphic, 4-loculate, basifixed, placed just below the petal tip, at 2 different heights, sessile or nearly so, sometimes with a small connectival horn; style straight (the upper portion convoluted in female *P. polystachyum* and *P. tortistylum* (Kuijt) Kuijt); style absent in male flowers (*P. peruviense* (Kuijt) Kuijt, *P. roraimense*, and *P. polystachyum*) or present (in other species); stigma capitate, often oblique; anthers/staminodia absent in female (*P. roraimense*) or present (in other species). Fruit a 1-seeded berry, the seed enveloped by viscin, endosperm present, hexangular at least in *P. leptostachyum* but unknown in others, embryo dicotyledonous, slender, torpedo-shaped, the radicular pole not swollen. Pollen grains oblate, and moderate in size, the amb basically triangular (see the discussion below).

Distribution. *Peristethium* is a genus of 15 species, ranging from northern Amazonian Bolivia and adjacent Brazil (Acre) through Peru, Ecuador, Colombia, and Venezuela, and into Panama and Costa Rica, with one endemic species on Mt. Roraima, and a second rare species in the nearby Pakaraima Mountains (Fig. 1).

Etymology. The genus name is taken from the Latin for "peri-," meaning "surrounding, around," and "-stethium" for "collar or involucre."

Discussion. In addition to the generic characters in the above description, the anatomical circumscription of *Peristethium* is apparently significant. Foliar sclerenchyma appears to supply another generic distinction from *Struthanthus*, but I can provide only a glimpse of this feature. The presence of astrosclereids in the mesophyll of *P. leptostachyum* (as *S. leptostachyus*), in contrast to nearly all other *Struthanthus* species, was first mentioned in Kuijt (1964). The possible taxonomic utility of foliar sclereids was then raised with reference to some of the species placed in *Peristethium* (Kuijt, 1981b). *Peristethium roraimense* is especially noteworthy in this regard, as much of its leaf mesophyll consists of astrosclereids with many bulbous arms (noted as *Cladocolea roraimensis*; Kuijt, 1975b). Foliar sclereids are known to occur also in a couple of unrelated Mexican *Struthanthus* species (Kuijt & Lye, 2005), but are not of the same type. At present, the occurrence of foliar astrosclereids seems to buttress the taxonomic integrity of *Peristethium*.

Pollen. I have been able to study the pollen of three species, *Peristethium aequatoris*, *P. leptostachyum*, and *P. lojae*, and significant palynological differences exist between species even in such a modest sample (Fig. 2). The first two species are generally similar, but *P. lojae* is different in several respects. This is interesting in that it fully supports its separate status as a species, a question that was by no means securely established in Kuijt (1986), where the suspicion remained that *P. lojae* might be no more than an extreme form of *P. leptostachyum*. The pollen of all three species reported here is oblate and moderate in size (slightly more than 20 μm diameter). The outline of the pollen grain in polar view, or amb (Erdtman, 1952), is basically triangular, that of *P. aequatoris* and *P. leptostachyum* sometimes slightly concave, and that of *P. lojae* more commonly a little convex. The surface in all three species is essentially psilate, being very slightly verrucate between lobes. The margo is especially smooth and somewhat raised. *Peristethium aequatoris* and *P. leptostachyum* have isopolar pollen, but the situation in *P. lojae* is not clear. Micrographs for *P. lojae* show many grains with a distinctive, psilate apocolpial field, but many others without. I have established that at least some individual grains are heteropolar in this respect. It is not possible at this time to ascertain whether this is true for all grains. The variation in the size, shape, and prominence of the apocolpial field urges caution in this regard. The *P. lojae* apocolpial field ranges from circular to nearly triangular and is also somewhat variable in size. The grains of *P. aequatoris* and *P. leptostachyum* differ from each other in that the colpae of the former are wide, yet so shallow as to be inconspicuous, and the equatorial areas between lobes are a little more roughly ornamented than in *P. leptostachyum*. In both cases we are concerned with a diploporate condition. A polar view of many *P. aequatoris* grains demonstrates that the colpae are so shallow as to leave some uncertainty of their polar fusion (Fig. 2A). The pollen grains of *P. lojae* can immediately be recognized as being different from those of the other two species studied here. The colpae are transequatorial and very deep, with distinctly raised, smooth margins along their full length. Thus a polar view shows deeply notched lobes (Fig. 2C, D). The grains of *P. lojae* have three rather than six pores, each situated at the equator. The striking apocolpal fields described above also clearly separate *P. lojae* from the other two species studied. Apocolpal fields such as that of *P. lojae* have previously been reported from several other small-flowered, Neotropical genera (Feuer & Kuijt, 1985), as has heteropolarity, sometimes in the same population as isopolarity.

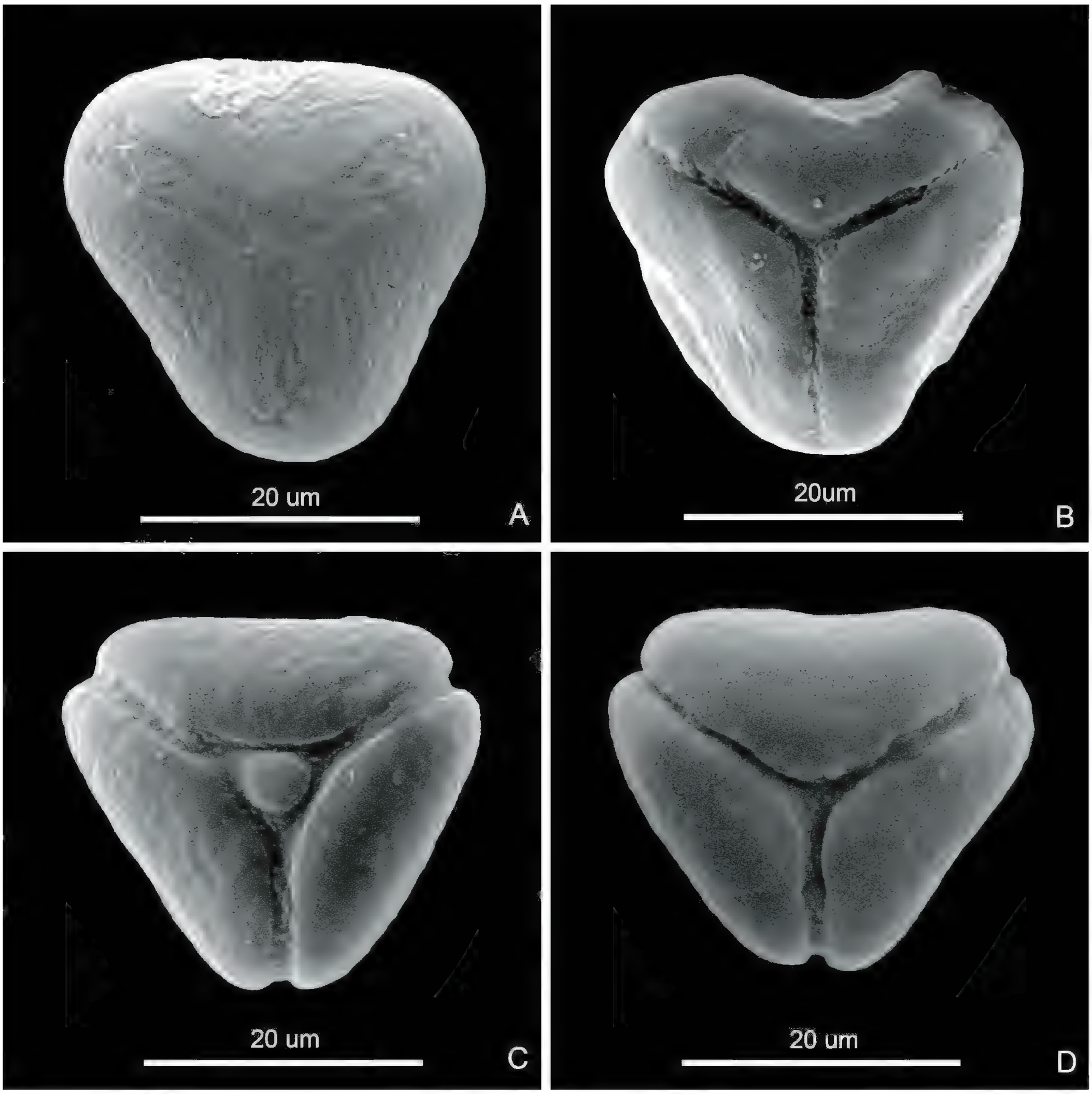

Figure 2. Representative pollen grains in polar view in *Peristethium* species. —A. *P. aequatoris* (Kuijt) Kuijt (*Van der Werff & Gudiño 107033*, UC). —B. *P. leptostachyum* (Kunth) Tiegh. (*Foster & Terborgh 6166*, UC). —C, D. *P. lojae* (Kuijt) Kuijt, showing two opposite polar views (*Lewis et al. 2953*, UC).

Sex distribution. The sex distribution in species of *Peristethium* continues to be ambiguous in some cases, partly because the anthers are exceedingly small at least when compared to those of other Neotropical genera, especially *Struthanthus*. It is only when fruiting specimens also carry evident, pollen-bearing anthers that flowers can be securely regarded as bisexual as in *P. archeri*. Similarly, a species is clearly dioecious where the anthers or styles are completely missing in some specimens, as exemplified in *P. peruviense*, *P. roraimense*, and (at least most) *P. polystachyum*. Monoecious species are unknown in Neotropical Loranthaceae, except in two *Oryctina* Tiegh. species (Kuijt, 1981a) and (questionably) in *Cladocolea coriacea* Kuijt (Kuijt, 1987b). It is thus certain that both dioecious species and species with bisexual flowers coexist in *Peristethium*. The same duality characterizes *Cladocolea* and the genus previously known as *Phthirusa* Mart. (Kuijt, 1975b, 2011b). Unfortunately, there remain some species in *Peristethium* where limited materials do not allow us to ascertain sexual distribution, therefore sex distribution is not utilized in the keys below.

Summary of distinctive features. Since most species of *Peristethium* have earlier been placed in *Struthanthus* or *Cladocolea*, it is useful to underline

the distinctive features of the genus *Peristethium*. The most significant of these is the cluster of mostly chartaceous and caducous bracts at the base of the inflorescence and this aspect is striking on at least the larger species. No species of *Struthanthus* or *Cladocolea* has such obvious bracts. The unrelated, monotypic genera *Gaiadendron* G. Don and *Panamanthus* have minute bracts at the base of the inflorescence, but these are not chaffy, and are not followed by similar, caducous bracts in the rest of the inflorescence. The minute, basifixed anthers, placed well above the petal's middle, are either sessile or on exceedingly short filaments, as seen on upper anthers. The androecium in *Peristethium* is also distinctive, even though sessile anthers occur exceptionally in *Struthanthus*, as in *S. condensatus* Kuijt (Kuijt, 1980: fig. 18), in some *Passovia* species (Kuijt, 2011b), and in *Cladocolea* (e.g., *C. alternifolia* (Eichler) Kuijt; Kuijt, 2003a). As seen in *Peristethium*, the subterminal monads and terminal flowers are known only in one Mexican species of *Struthanthus*, *S. deppeanus* (Kuijt, 1981b: figs. 4.2–4.3), but predominate in *Cladocolea*. Triads are not known in *Cladocolea* except for one probably teratological instance in *C. pedicellata* Kuijt (Kuijt, 1975b: fig. 28b). The pentads of *P. confertiflorum* are unique in the family. Finally, the slender embryo and angular endosperm are at least very unusual in New World Loranthaceae, but have not been documented for all *Peristethium* species. A striking feature without equivalence in other Loranthaceae is the absence of even a rudimentary style in most or all male flowers of three species, *P. peruviense*, *P. polystachyum*, and *P. roraimense*. In these species, the base of the flower shows a circular cushion, probably a nectary, with a small, central depression. Otherwise, the solitary, other instance may be the taxonomically isolated *C. coriacea* from Venezuela (Kuijt, 1987b), where the lack of a style in male flowers has not been documented convincingly.

Another, but perhaps more subtle contrast between *Struthanthus* and *Peristethium* is the sequence in which flowers open. As pointed out in an earlier survey of the Loranthaceae (Kuijt, 1981b), indeterminate inflorescences flower exclusively from the base upward and, in long inflorescences, young or mature fruits may be in evidence at proximal nodes while distal flowers are still in bud. Determinate inflorescences, in contrast, develop basipetally and tend to open the terminal flower first, or all the flowers will open more or less simultaneously. The latter is especially evident in *P. confertiflorum*, *P. leptostachyum*, and *P. polystachyum*.

The shape of the mature *Peristethium* embryo has emerged as a distinctive generic character. In all species of *Struthanthus* (and many *Dendropemon*, *Oryctanthus* (Griseb.) Eichler, and *Passovia* species) seen by me, especially at the time of fruit maturation, the young seedling or embryo has a massively expanded haustorial disk (Kuijt, 1982). Nothing of the sort is true in *P. archeri* (described herein), *P. colombianum* Kuijt (Fig. 6E), *P. leptostachyum*, *P. polystachyum* (Fig. 15E), or *P. primarium* in which the radicular pole is slender and not in the least expanded (Kuijt, 1975a: fig. 2d; 1987a: fig. 5b). The seedling at that stage is torpedo-shaped, lacking any expansion of the radicular, haustorial pole. The seedling of *Cladocolea* is somewhat similar but is not as narrow and slender as that of *Peristethium* (Kuijt, 1975a). Other Neotropical but unrelated genera with slender embryos are *Gaiadendron*, *Notanthera* (DC.) G. Don, *Panamanthus*, and *Tripodanthus* (Eichler) Tiegh. (Kuijt, 1982).

In female (i.e., fruit-bearing) specimens of *Peristethium aequatoris*, which make up the great majority of specimens seen, the anthers are fully formed but exceedingly small and clearly do not contain pollen, even though the sterile pollen sacs seem to open. In both this species and some others, sex distribution may thus be difficult to ascertain. A plant with all flowers in the fruiting stage cannot reveal whether it is a female plant or whether its flowers are bisexual.

Epicortical roots, as stated in the above generic description, have been noted in at least two species. Those in *Peristethium archeri* may be at least 25 cm (*Neill et al. 5909*, UC) and may reach several meters in *P. leptostachyum* as noted in Costa Rica and Panama (Kuijt, 1964).

Because of the several generic changes that have occurred in the group in recent decades, Table 1 is provided to facilitate the identification of specimens.

Taxonomic Key to the Species of *Peristethium*

1a. Leaf apex rounded to slightly emarginate; petals 5; known from the Pakaraima Mountains only ..... 9. *P. nitidum*
1b. Leaf apex not rounded or emarginate; petals 4 or 6; not known from the Pakaraima Mountains.
  2a. Inflorescence bearing monads only; flowers tetramerous.
    3a. Flowers on pedicels as long as the ovary; shoots apparently determinate, the apex aborting; known only from northern Peru (San Martín) and adjacent Ecudaor ..... 11. *P. peruviense*
    3b. Flowers sessile; shoots percurrent; northern Peru to Colombia, or Mt. Roraima.

Table 1. Morphological comparison of genera within the *Struthanthus* complex. M = Monads, T = triads, NA = not applicable.

	Inflorescence type	Monads or triads	Bracteoles on monads	Plant sexuality	No. of petals	Basal inflorescence bracts
Cladocolea Tiegh.	det.*	M	–	bisexual/dioecious	(4)6(5)	–
Dendropemon (Blume) Rchb.	indet.	M	+	bisexual	6	–
Maracanthus Kuijt	indet.	M	+	bisexual/dioecious	6	–
Oryctanthus (Griseb.) Eichler	indet.	M	+	bisexual	6(4)	–
Oryctina Tiegh.	indet.	M	+	bisexual/dioecious/ monoecious	6	–
Panamanthus Kuijt	indet.	M	+	bisexual	6	–
Passovia H. Karst.	indet.	T	NA	bisexual/dioecious	6(4)	–
Peristethium Tiegh.	det.	M/T	–	bisexual/dioecious	4(6)	+
Phthirusa Mart.	NA	T	NA	bisexual	4	–
Pusillanthus Kuijt	indet.	T	NA	bisexual	4	–
Struthanthus Mart.	indet.*	T	NA	dioecious	6*	–

*Exceptions occur in species within these genera.

4a. Leaves coriaceous, apex rounded to emarginate, venation obscure; known only from Mt. Roraima ..... 14. *P. roraimense*

4b. Leaves thin or somewhat coriaceous, apex acute to attenuate, venation evident; northern Peru to Colombia.

5a. Leaves to 16 cm, thin, apex long-acuminate, lowest lateral veins not especially prominent; inflorescence mostly < 1 cm ..... 3. *P. attenuatum*

5b. Leaves < 10 cm, somewhat coriaceous, apex abruptly acute to nearly obtuse, lowest lateral veins prominent, reaching at least to the middle of the blade; inflorescence 3–4 cm ... . 2. *P. archeri*

2b. Inflorescence bearing triads and (some species) subterminal monads; flowers hexamerous or tetramerous.

6a. Lateral triad flowers as well as monads and triads short-pedicellate ..... 1. *P. aequatoris*

6b. All flowers and triads sessile or essentially so (but see *P. confertiflorum*).

7a. Flowers tetramerous; style straight; Panama ..... 13. *P. primarium*

7b. Flowers hexamerous; style straight, convoluted, or lacking; Costa Rica to Bolivia.

8a. Triad pairs 15 to 24 per inflorescence, densely crowded; some pentads in mid-region of the inflorescence; both triads and pentads deflected, on short, stout peduncles; Peru .... 5. *P. confertiflorum*

8b. Triad pairs 12 or fewer, not densely crowded; pentads lacking; both triads and monads sessile, not deflected; Costa Rica to Bolivia.

9a. Flowers sunken in raised nodal cups, the subtending nodes swollen especially in fruit; style known to be usually lacking in the male flower and strongly convoluted in the female ..... 12. *P. polystachyum*

9b. Flowers not sunken in nodal cups, subtending nodes not swollen; both male and female flowers with straight styles (except in *P. tortistylum*), or style unknown.

10a. Subterminal monads mostly 2 to 8 pairs.

11a. Internodes terete; inflorescences becoming ca. 4 cm; style strongly contorted ..... 15. *P. tortistylum*

11b. Internodes quadrangular or keeled; inflorescence up to 8 cm (as inferred from infructescence length); style unknown ..... 10. *P. palandense*

10b. Subterminal monads 1(to 2) or lacking.

12a. Internodes on leaf-bearing stems 1 cm thick, with small, pustular lenticels; knoblike growths developing in leaf axils; inflorescences apparently lacking terminal flower and subterminal monads; inflorescence axis lacking lenticels ..... 6. *P. lamprophyllum*

12b. Internodes on leaf-bearing stems mostly 0.5 cm thick or less (but see *P. colombianum*), with pustular or elongated lenticels; inflorescence axis developing prominent lenticels in fruit; knoblike growths in leaf axils absent; inflorescences with terminal flower and 1 or 2 pairs of subterminal monads.

13a. Infructescences much crowded; leaf-bearing internodes 1 cm thick, developing numerous slender, elongated lenticels; western Colombia ..... 4. *P. colombianum*

13b. Infructescences not obviously crowded; leaf-bearing internodes mostly 0.5 cm thick or less, developing pustular lenticels; Costa Rica to Ecuador.

14a. Leaves darkening when dry; fruit obovoid; pollen heteropolar, with apocolpial field on one pole; southern Andean Ecuador ..... 8. *P. lojae*

14b. Leaves remaining green when dry; fruit ellipsoid; pollen isopolar, lacking apocolpial field; Costa Rica to Ecuador ..... 7. *P. leptostachyum*

1. Peristethium aequatoris (Kuijt) Kuijt, comb. nov. Basionym: *Struthanthus aequatoris* Kuijt, Fl. Ecudaor, 24: 149–151. 1986. TYPE: Ecuador. Pichincha: Cantón Quito, along rd. betw. Tandayapa & Mindo, 9–10 km beyond Tandayapa, 2530 m, 16 Dec. 1979, *T. B. Croat 49355* (holotype, MO-3096226!; isotypes, UC-1956802!, UC-1956803!). Figure 3.

Plants dioecious, leggy, sparsely branched, glabrous; internodes straight, slightly quadrangular to carinate, smooth without lenticels, to 9(13) cm; bearing occasional basal epicortical roots. Leaves to 12 × 10 cm, thin, broadly lance-ovate to nearly elliptical, apex obtuse to abruptly attenuate-cuspidate or slightly acuminate, base mostly truncate, venation pinnate, evident, with 2 to 4 or more lateral veins reaching at least halfway to the apex, midvein running into the apex; petiole 1–1.5 cm. Inflorescences 1 to 3 per leaf axil, each inflorescence largely triadic, 5–14 cm; inflorescence bearing 8 to 14 pairs of triads followed by 1 pair of monads, and 1 terminal flower; triad and monad peduncles 1–2 mm, median flower of triads sessile, lateral flowers on pedicels ca. 1 mm; basal inflorescence bracts several pairs, small, ± persistent; floral bracts and bracteoles caducous; peduncle 1–2 cm. Flowers hexamerous, flower buds yellowish or greenish white, apex rounded, 6.5 mm; petals ca. 4.5 mm; male flower with anthers nearly 1 mm, at 2 different heights near the bud apex, not overlapping, with slender style and undifferentiated stigma; female flower as the male but more slender, sterile anthers 1 mm, well-formed and even dehiscing; style 4 mm; stigma capitate. Fruit an ovoid berry, dull orange-red, to 10 mm and 5.5 mm thick when mature.

Distribution. Collections of *Peristethium aequatoris* have been seen only from Colombia. It grows in elevations ranging from 160 to 4000 m.

Discussion. The protologue of *Struthanthus aequatoris* (Kuijt, 1986) contained some errors that must be corrected. Most importantly, *Peristethium aequatoris* does indeed have chaffy bracts at the base of the inflorescence, but they are small and early caducous, and are obvious only at the earliest stages of inflorescence development. Similar, but somewhat smaller, caducous chaffy bracts subtend the triads and monads and can be seen at the tip of expanding inflorescences. In the protologue it was suggested that the species might also be present in neighboring Colombia. This is indeed the case, as numerous collections cited below indicate.

Additional specimens examined. COLOMBIA. **Caqueta:** 63 km N of Florencia near border with Huila, *Gentry et al. 9181* (MO). **Chocó:** Cerro del Torrá, *Silverstone-Sopkin et al. 4454* (MO, UC); carr. Ansermanuevo–San José del Palmar, border of Valle del Cauca, Alto del Galápago, *Forero et al. 2882* (MO). **Nariño:** Mpio. Ricuarte, Corregimiento Chucunéz, Reserva Natural La Planada, *Roldán 1603* (UC); 7 km from Chucunés, 1°5′N, 78°1′W, *Gentry & Keating 59728* (MO); Reserva Natural La Planada, a 7 km de Chucunés, *Benavides 8709* (MO); Corregimiento Chucunés, Reserva Natural La Planada, *Roldán 1601* (HUA, MO), *1602* (MO), *1603* (MO); trail from La Planada to Pielapí, 1°4′N, 78°2′W, *Gentry et al. 63655* (MO); Isla de los Osos, 1°10′N, 77°50′W, *Benavides 9733* (MO); trayecto San Isidro–La Planada, 1°10′N, 77°58′W, *Benavides 9230* (MO). **Riseralda:** Santa Rosa de Cabal, along rd. to Termales, borders of Río San Eugenio, *Wijninga & Wolf 548* (UC). **Santander del Sur:** 4 km below Palo Blanco W of Vélez, *Luer et al. 10103* (MO, UC). ECUADOR. **Carchi:** Mira, 0°50′N, 78°11′W, *Tirado et al. 1282* (UC); above Maldonado, *Van der Werff & Gudiño 10858* (UC); Tulcán–Maldonado, W of Tufino, *Van der Werff & Gudiño 10703* (UC). **Cotopaxi:** Cantón Sigchos, 35 km de Sigchos, 0°32′4″S, 78°58′43″W, *Ramos et al. 6862* (UC). **Morona-Santiago:** Cantón Gualaquiza, Cordillera del Cóndor, 3°27′S, 78°22′W, *Gentry 80344* (UC). **Napo:** SW of Cosanga, Orellana, Parque Nac. Yasuní, 0°30″S, 77°52′W, *Dik 476* (UC). **Pichincha:** vic. of Bellavista Scientific Research Station and 1.2 km S of Bellavista, 0.3–1 km W of Tandayapa–Mindo rd., 00°01′16″S, 78°41′07″W, *Croat et al. 96475* (MO, UC); 1.7–2.1 km beyond Bellavista, 0°01′02″S, 78°44′07″W, *Croat 94632* (MO, UC); Tandayapa–Mindo rd., 7.2 km S of Tandayapa, 0°0′24″S, 78°40′W, *Croat et al. 96505* (MO, UC); vic. of Bellavista, Km. 12 on rd. from Tandayapa to Mindo, 0°01′02″S, 78°44′49″W, *Croat 94573* (MO, UC); carr. Nanegalito–Armenia, Loma de San José, La Vuelta Brava, 0°5′N, 78°40′W, *Zak & Jaramillo 3221* (K ex MO); carr. Quito–Mitad del Mundo, Calacalí–Nanegalito, betw. Calacalí & Nanegalito, *Freire-F. et al. 631* (NY); Cantón Quito, 0°4′N, 78°39′W, *Webster et al. 30484* (UC); old rd. Quito–

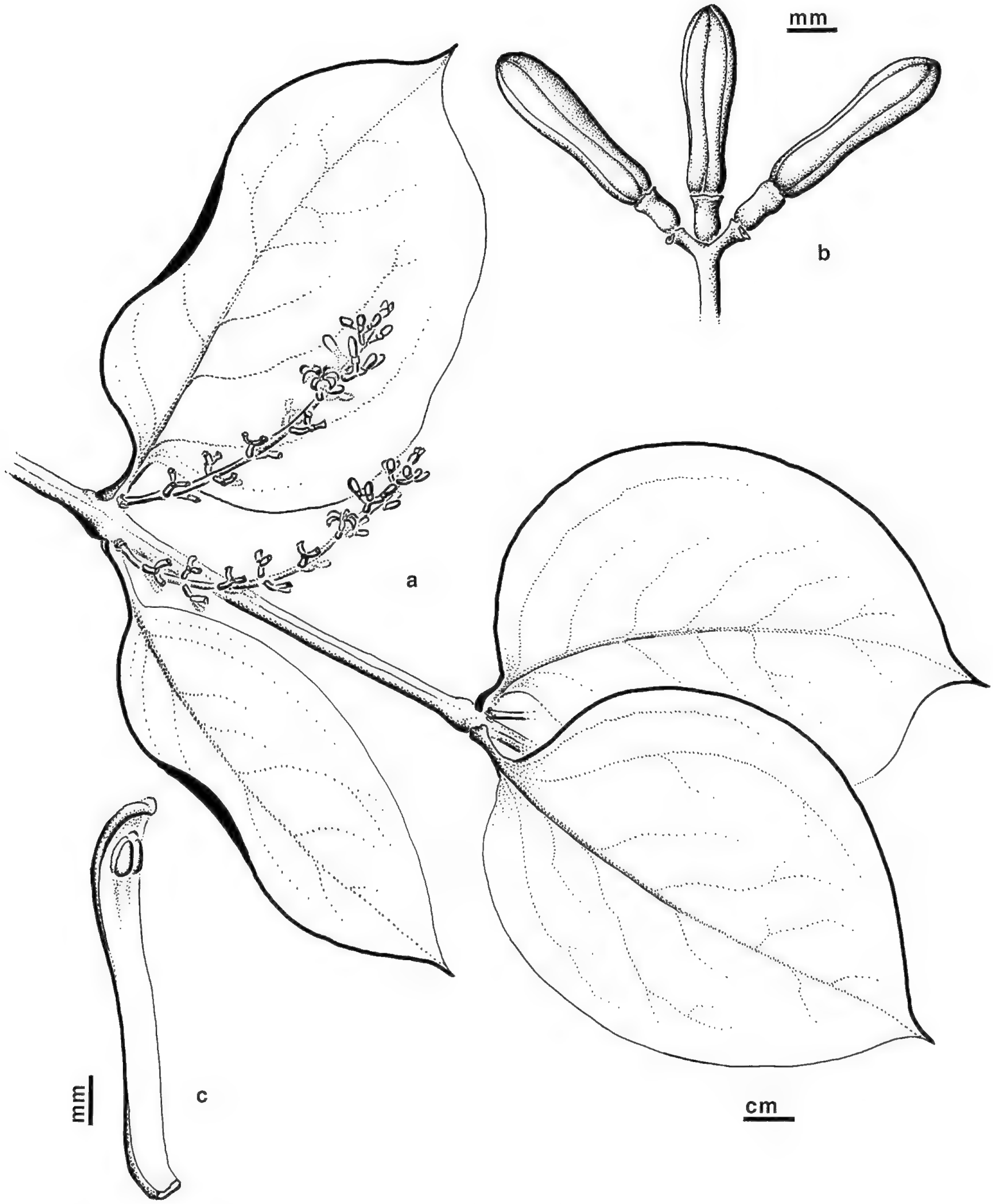

Figure 3. *Peristethium aequatoris* (Kuijt) Kuijt. —A. Habit. —B. Triad. —C. Petal and stamen. Drawn from *Croat et al. 96475* (UC). Scale bars: A = 1 cm; B, C = 1 mm.

Santo Domingo de los Colorados, 6–11 km W of San Juan de Chiriboga, 0°15′S, 78°45′W, *Luteyn & Boom 8479* (NY, UC); 0°13′53″N, 78°48′10″W, *Zak 1102* (K, UC); *1155* (UC); Reserva Río Guajalito, near Chiriboga, along old rd. Quito–Santo Domingo, on Lauraceae, *Van der Werff et al. 12218* (F, UC); carr. Quito–San Juan–Chiriboga, Empalme, Km. 59, *Zak 1205* (K, UC); *1307* (UC); carr. Quito–Chillogallo–San Juan–Chiriboga, 29–32 km from Chillogallo, 0°17′S, 78°41′W, *Freire-F. et al. 1514* (NY); old rd. Quito–Nono, Mindo, 9 km S of Tandayapa toward Mindo, 0°N-S, 78°43′W, *Luteyn et al. 8834* (NY); Reserva Florística-Ecológica Río Guajalito, Km. 59 de la carr. antigua Quito–Santo Domingo de los Colorados rd., estribaciones occidentales del Volcán Pichincha, 0°13′53″S, 78°48′10″W, *Jaramillo & Zak 7916* (K ex MO, UC); main entrance from Quito–Santo Domingo rd., 3.5 km from hwy., *Croat 72027* (MO). **Zamora–Chinchipe:** Zamora, *Palacios & Tirado 13400* (UC).

2. Peristethium archeri (A. C. Sm.) Kuijt, comb. nov. Basionym: *Oryctanthus archeri* A. C. Sm., Bull. Torrey Bot. Club 59: 516–517. 1932. *Cladocolea archeri* (A. C. Sm.) Kuijt, J. Arnold Arbor. 56: 277–281. 1975. TYPE: Colombia. Antioquia: 18 km N of Medellín, 2000 m, Jan. 1931, *W. A. Archer 1521* (holotype, US-0151740!). Figure 4.

Plants rather large, glabrous, percurrent; stems long and straight, branching only from older wood, angular and smooth when young, becoming stout and terete, with numerous conspicuous, round lenticels of uniform size; internodes 4.5–8 cm; epicortical roots present at the base, occasionally on the stems, to 25 cm. Leaves decussate, 3–10 × 2–5 cm, somewhat coriaceous, ovate, apex abruptly acute to nearly obtuse, base rounded to truncate, midvein prominent as a groove, running into apex, with prominent lateral veins, the lowest ones often running more than halfway to the apex; petiole 4–8 mm, canaliculate. Inflorescences several per leaf axil; each inflorescence mostly 3–4 cm, with ca. (3 to)5 pairs of ebracteolate, sessile monads and a single terminal flower; floral bracts acute, to nearly 3 mm, naviculate, mostly caducous but some persisting; with several pairs of small, chartaceous scale leaves at the base. Flowers tetramerous, bisexual, sessile, yellowish green, the mature bud nearly 6 mm, blunt; petals 4.5 mm, 4(or 5); each with 1 sessile anther, anthers placed at 2 different heights, both above the middle but all of similar shape, having 4 pollen sacs with blunt projecting connective; pollen smooth, somewhat 3-lobed but lacking evident surface markings; ovary 1.5 × 1.5 mm, with irregularly denticulate calyculus; style straight and rather stout, 3 mm; stigma weakly differentiated, oblique. Fruit ovoid, "rose red when young, becoming blue with greyish bloom" (*Archer 1521*, in sched.), 6 × 4 mm thick, with blunt apex; embryo dicotylous, 3 mm, narrow, the radicular pole not expanded.

Distribution. Collections of *Peristethium archeri* have been seen only from Colombia. This species grows in elevations ranging from 500 to 2500 m.

Dicussion. The original concept of *Peristethium archeri* (Smith, 1932) and my subsequent description and illustration for the *Flora of Ecuador* (Kuijt, 1986) were based on northern material, the type from Colombia. It has since developed that the species is exceedingly variable further south in Ecuador, both in leaf shape and the size of inflorescences, and intermediates to *P. attenuatum* Kuijt may occur.

Peristethium archeri, as here circumscribed, is a variable species in terms of leaf shape and inflorescence size and composition. Its possible intermediates to *P. attenuatum* are alluded to below. In Colombia (especially in Antioquia), a very small form occurs that may, in fact, represent an unrecognized species. Its leaves are no more than 6 × 2 cm and are narrowly ovate with an attenuate apex and obtuse base. Most strikingly, its inflorescences and infructescences (including flowers and fruits) are at most 1 cm, are completely sessile in the leaf axils, and regularly bear only seven flowers, including the terminal one. Below, I list the two most striking specimens I have encountered and that I place in *P. archeri* only provisionally; they were collected in essentially the same locality (*Roldán et al. 747* and *1120*, MO). Possible intermediates to larger *P. archeri*, also from Antioquia, have been noted, as in *Roldán 1063* (MO). In the first specimen, fruits are described as orange and black, in the second, pink to black.

Additional specimens examined. COLOMBIA. **Antioquia:** Mpio. Frontino, carr. Nutibara–La Blanquita, Sector Murrí, 6°45′N, 76°21′W, on Compositae, *Roldán et al. 747* (MO); Km. 14, on Ericaceae, *Roldán et al. 1120* (MO); La Sierra, 18 km N of Medellín, on *Tournefortia fuliginosa* Kunth, *Archer 1058* (US); Cordillera Central, near Porcesito, Río Medellín valley, *Hodge 6842* (US). **Chocó:** Mpio. Carmen de Atrato, 6°1′N, 76°7′W, *Roldán & Luteyn 1054* (UC). **Nariño:** 1°15′N, 78°9′W, *Gentry et al. 55201* (UC). **Valle:** Mpio. Cairo, Cerro del Ingles, Cordillera Central, Serranía de las Paraguas, *Silverstone-Sopkin et al. 2753* (F); shores of Río Bugalagrande, Calamar, *Cuatrecasas 20506* (F); Cordillera Occidental, W slope, Hoya del Río Dagua, La Elsa, La Cristalina, *Cuatrecasas 15244* (F, UC); Hoya del Río Cali, Quebrada Honda, camino a Miralindo, *Cuatrecasas 18430* (F); Paraguas, cerca de frontera con Dpto. Chocó, *Silverstone-Sopkin 3837* (F). **San Pablo:** Km. 16, Cali–Buenaventura, *Restrepo 24* (UC); Finca Zingara, Km. 18, *Restrepo 6* (UC). ECUADOR. **Imbabura:** Lita, *Acosta Solís 12200* (F), *Madison et al. 4999* (SEL). **Morona-Santiago:** Cantón Huamboya, Shankaimi, 1°58′S, 77°49′W, *Palacios 11418* (MO, UC). **Pastaza:** Mera, *Harling et al. 9845* (S); on *Miconia* Ruiz & Pav., *Asplund 19166* (S). **Pichincha:** near Santo Domingo, *Fagerlind & Wibom 1758* (S); Chaupi, *Dodson & Thien 1852* (UBC, UC). **Tungurahua:** Río Negro, bank of Río Pastaza, on *Banara guianensis* Aubl., *Asplund 18624* (S). **Zamora-Chinchipe:** Cantón Zamora, Romerillos Bajo, E border of *Podocarpus* Natl. Park, Quebrada Neya, Fundación Maquipucuna, 4°11′S, 78°55′W, *Clark et al. 3337* (MO, UC); El Pangui, Cordillera del Cóndor, near Cóndor military post, on Ecuador–Peru border, 3°38′20″S, 78°23′29″W, *Neill et al. 14516* (UC ex MO). PERU. **Amazonas:** Bagua, 4°55′S, 78°19′W, *Rodríguez et al. 1012* (UC); Imaza, *Díaz et al. 7972* (UC). **Cuzco:** Paucartambo, *Nuñez 8076* (UC). **Huánuco:** Prov. Pachitea, near Pucallpa, *Wallnöfer 18–26388* (UC); SW slope of Río Llulla Pichis watershed, ascent of Cerro La Sira, on Melastomataceae, *Dudley 13450* (F). **Piura:** Prov. Huancabamba, *Díaz et al. 2751* (UC).

Figure 4. *Peristethium archeri* (A. C. Sm.) Kuijt. —A. Habit. —B. Young inflorescence. —C. Young infructescence. —D. Bud and floral dissection. A, B, and D drawn from *Palacios 11418* (UC); C drawn from *Neill et al. 14516* (UC). Scale bars: A = 1 cm; B–D = 1 mm.

3. Peristethium attenuatum Kuijt, sp. nov. TYPE: Peru. Amazonas: Prov. Bagua, Distr. Imaza, Tayu Mujaji, Comunidad de Wawas, sobre una capa esponjosa de raices y materia orgánica, Campau Uwejush, 5°15′56″S, 78°22′07″W, 1200 m, 21 Oct. 1997, *R. Vásquez, Lirio & Pitug 24633* (holotype, MO-4922779!). Figure 5.

Haec species quoad surculos percurrentes, inflorescentiam monades tantum gerentem, bracteas persistentes etiam flores sessiles bisexuales tetrameros *Peristethio archeri* (A. C. Sm.) Kuijt arcte affinis, sed ab eo foliis tenuibus majoribus apice plerumque attenuatis venis lateralibus basalibus non elevatis, inflorescentia breviore atque calyculo inconspicuo distinguitur.

Plants percurrent, glabrous; internodes 3–6 cm, terete (somewhat quadrangular in coastal Ecuador), bearing reddish brown, pustular lenticels when young. Leaves to 16 × 5 cm, paired, ovate, thin, apex long-acuminate, base truncate-cordate, venation pinnate, midvein running into the apex, lateral veins obscure; petiole ca. 7 mm. Inflorescence 6–8 mm, determinate, not expanding in fruit; above with 3 pairs of ebracteolate, sessile monads, and a single terminal flower; flower bracts caducous; inflorescence bracts at least 4 pairs, acute, chaffy, persistent. Flowers sessile, bisexual, tetramerous, greenish white, 5 mm including 1 ovary, 1.5 mm with nearly smooth calyculus; petals 4.3 mm; anthers sessile, placed 2.5 mm above the base of the petals; style straight, 3 mm, placed on a small, raised portion; stigma capitate, distinct, oblique. Fruit 3 × 2 mm, ellipsoid, purplish or bluish green (*Vásquez et al. 34633*, in sched.), calyculus indistinct.

Distribution. Collections of *Peristethium attenuatum* have been seen from Ecuador and Peru. This species grows in elevations ranging from 100 to 1550 m.

IUCN Red List category. The conservation status of the new species is Data Deficient (DD) (IUCN, 2001).

Discussion. *Peristethium attenuatum* is closely related to *P. archeri* in having persistent inflorescence bracts, tetramerous bisexual flowers, and only monads. *Peristethium archeri* can be distinguished by having smaller, non-attenuate, thicker leaves and much longer, more floriferous and elongated inflorescences, and a distinctly erose calyculus. As mentioned under *P. archeri*, intermediates between it and *P. attenuatum* may occur.

Many of the Ecuadorian specimens cited below derive from northwestern Ecuador, being thus far removed (ca. 500 km) from the type locality, but they nevertheless seem to be conspecific with it, even though the young internodes are distinctly quadrangular rather than terete.

Paratypes. ECUADOR. **Carchi:** vic. of Peñas Blancas, 6.6 km N of El Chical along trail to Tobar Donosa, 0°58′38″N, 78°11′53″W, *Croat 94862* (MO, UC); along rd. betw. El Chical & Tulcán, 15.4 km E of El Chical, 0°54′04″N, 78°05′50″W, *Croat 94954* (MO, UC); Parroquia Tobar Donoso, Reserva Ethnica Awá Sabalera, 0°55′N, 78°32′W, *Aulestia et al. 759* (MO). **Esmeraldas:** Km. 8, Lita–Altotambo, *Dodson & Gentry 17542* (UC). **Quinindé:** Bilsa Biological Station, Montañas de Mache, 35 km W of Quinindé, 5 km W of Santa Isabela, Monkey Bone Trail, 0°21′N, 79°44′W, *Pitman & Bass 1084* (MO), *Pitman et al. 809* (MO); ridge of La Loma de los Guerrilleros, *Clark 2931* (MO); Río Palaví Awá encampment, 01°07′N, 78°37′W, *Hoover et al. 4073* (MO), 00°58′N, 78°16′W, *Hoover et al. 3102* (MO).

4. Peristethium colombianum Kuijt, sp. nov. TYPE: Colombia. Valle del Cauca: Mpio. Buenaventura, vía Buenaventura–Cali, 300 m, on *Cecropia* Loefl., 14 Apr. 2007, *D. Macias & B. R. Ramírez 5001* (holotype, CAUP!; isotype, CUVC!). Figure 6.

Haec species quoad habitum robustum atque folia grandia apice acuminata *Peristethio leptostachyo* (Kunth) Tiegh., quoad inflorescentiam magnam densissimam *P. confertifloro* Kuijt similis, sed a hoc inflorescentia pentadibus carente atque triadibus monadibusque sessilibus non deflexis, ab illo internodiis crassioribus lenticellis elongatis notatis, foliis in sicco fuscatis, inflorescentia magna densa squamis basalibus attenuatis subtenta atque bracteolis acicularibus triades monadesque subtendentibus distinguitur.

Plants quite robust, dioecious; stem internodes terete, bearing numerous, small, slender, elongated lenticels, to 7 cm and to 10 mm diam. when leaf-bearing. Leaves to 20 × 10 cm, leathery, lanceolate-ovate to nearly elliptical, apex acuminate, base truncate, dull on both sides, turning dark when dry, venation pinnate or nearly so, midrib strongly raised on abaxial side, running into apex, with 2 or more strong basal lateral veins; petiole 1 cm, stout. Male inflorescence at least 3 cm, axis quadrangular, bearing 7 to 9 pairs of triads, 1 or 2 pairs of subterminal monads with acicular bracteoles, and 1 terminal flower; female inflorescence subtended by at least 6 pairs of caducous, acute, brittle and stiff, papery scale leaves, to 8 cm in fruit, its axis to 2.5 mm thick at the base, with large lenticels, bearing up to 12 pairs of crowded, completely sessile triad pairs and 1 pair of subterminal monads, at least some with whiplike bracteoles 1 mm, followed by a single terminal, sessile flower. Flowers hexamerous, not

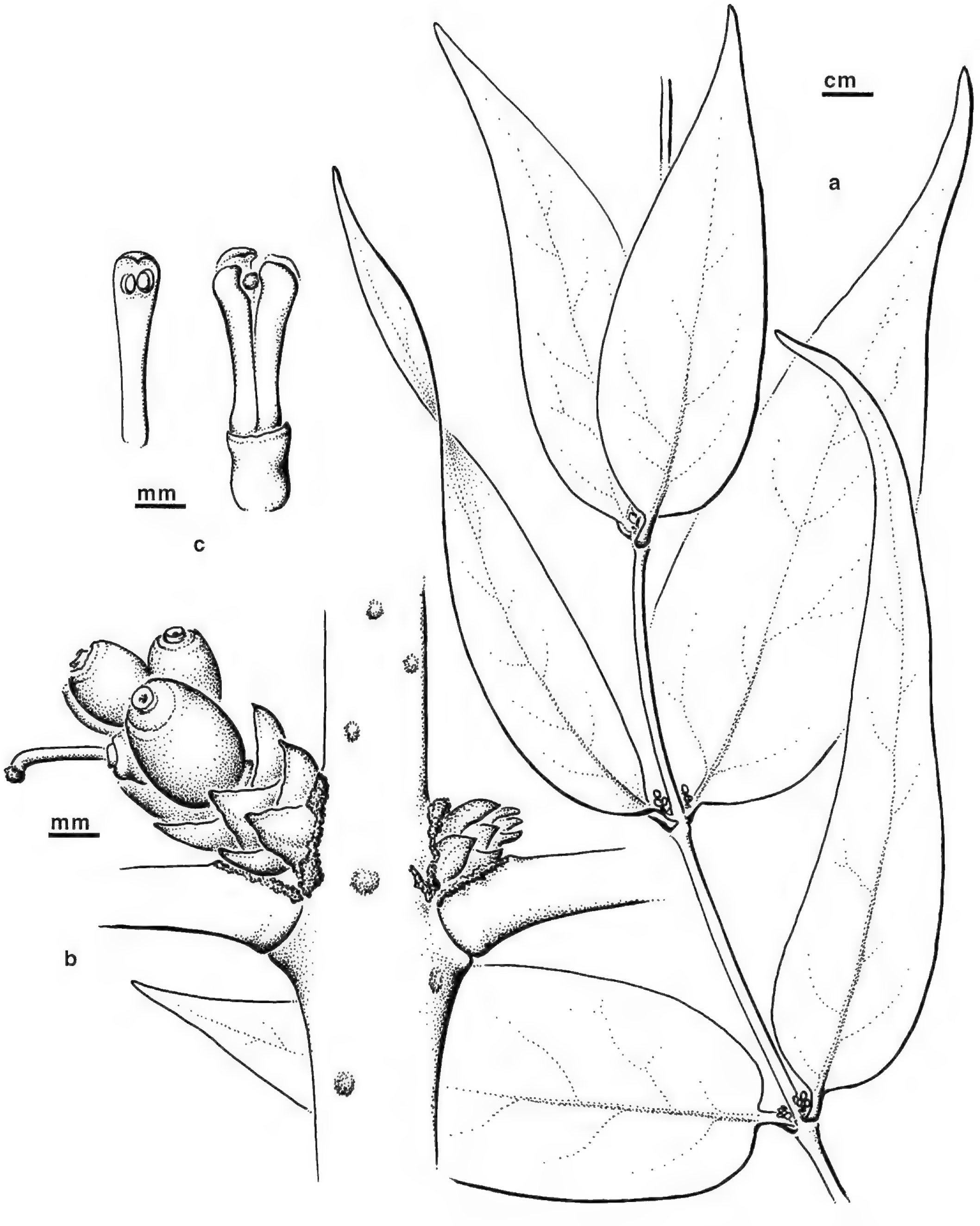

Figure 5. *Peristethium attenuatum* Kuijt. —A. Leafy shoot. —B. Infructescence. —C. Flower and petal. Drawn from *Vásquez et al. 34633* (MO). Scale bars: A = 1 cm; B, C = 1 mm.

placed in nodal cups, subtending nodes not swollen; male flower bud 5 mm, ovary 1 mm, with coarsely dentate calyculus; anthers 0.7 mm, slightly biseriate, sessile above the middle of the petals; sterile style nearly as long as the petals, slightly curved in the middle but essentially straight; stigma undifferentiated. Female flower unknown. Fruit ellipsoid to obovoid, reddish brown (*Macias & Ramírez P. 5001*, CAUP), 7 × 5 mm, apex truncate, calyculus inconspicuous; embryo 5 mm, extremely slender, the 2 cotyledons 2 mm, strap-shaped, the radicular end without swelling.

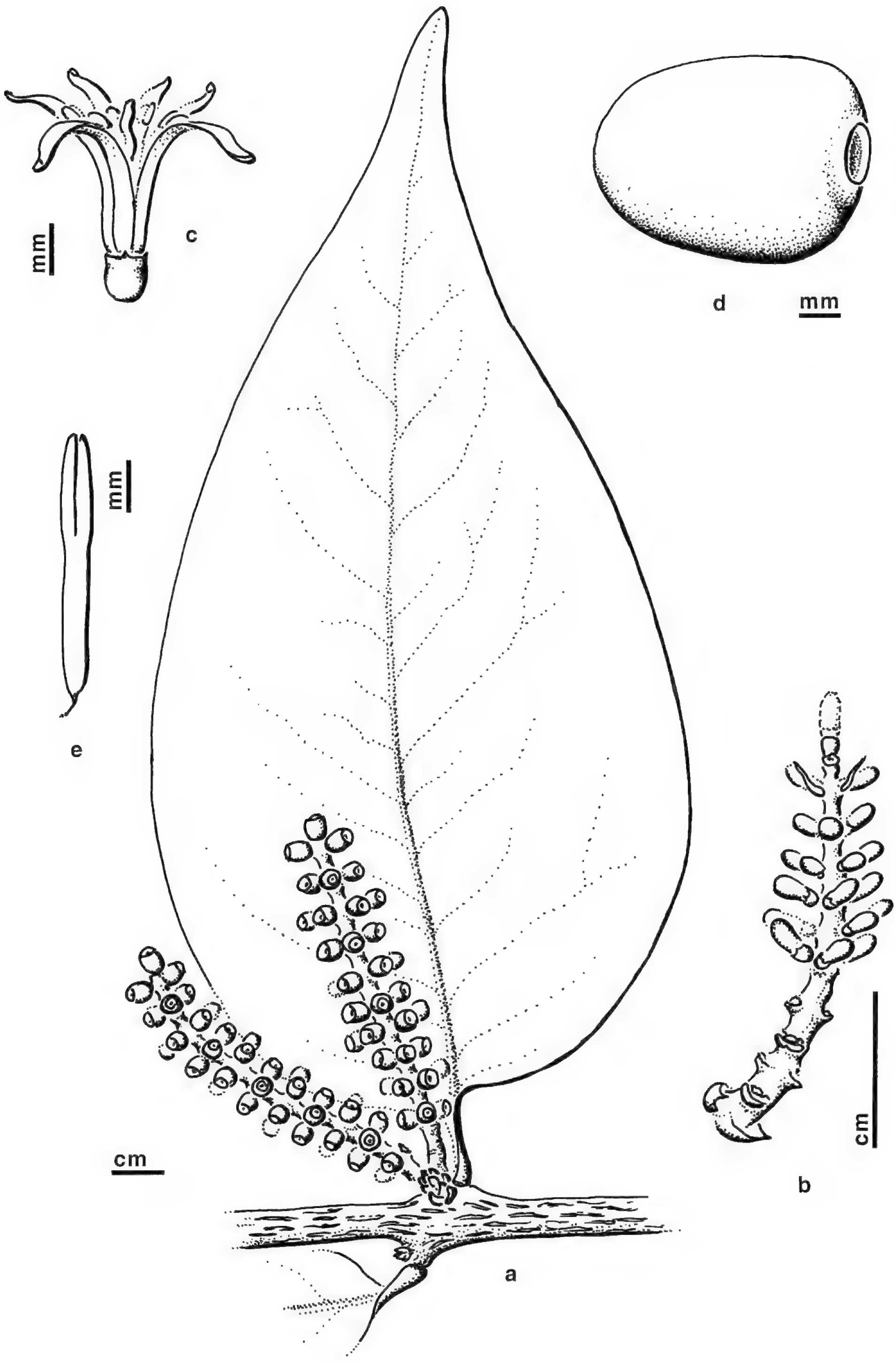

Figure 6. *Peristethium colombianum* Kuijt. —A. Habit and infructescences. —B. Male inflorescence —C. Open male flower. —D. Fruit. —E. Embryo. A, B drawn from *Macias P. & Ramírez P. 5001* (CAUP); C–E drawn from *Daly & Betancur 5344* (UC). Scale bars: A, B = 1 cm; C–E = 1 mm.

Distribution. Collections of *Peristethium colombianum* have been seen only from Colombia. This species grows in elevations ranging from 10 to 1700 m.

IUCN Red List category. The conservation status of the new species is Data Deficient (DD) (IUCN, 2001).

Discussion. It is unfortunate that the available material of this strikingly robust species lacks female flowers. The plants are similar to *Peristethium leptostachyum*, sharing a robust habit, similarly large leaves at least 18 cm long, with attenuate apices. *Peristethium colombianum* is distinguished by the massive, densely crowded infructescence axes with numerous triads; large, acuminate, dark-drying leaves are also distinctive, as are the attenuate basal scales of the inflorescence. In *P. leptostachyum*, there are many pairs of chaffy, pale bracts subtending the inflorescences, but acicular bracteoles subtend the triads and monads in *P. colombianum*. The only other known species of *Peristethium* with such large, densely crowded inflorescences is *P. confertiflorum*, which differs from *P. colombianum* in having distinct, deflected triad peduncles and occasional pentads. The fruits of the type are said to be reddish brown (*Daly & Betancur 5344*, in sched.), but this is likely an immature coloration, as the mature fruits are blue-purple, in at least most species of *Peristethium*.

Paratypes. COLOMBIA. **Antioquia:** Valley of Río Anorí, vic. of Planta Providencia, 35 km SW of Zaragoza, area surrounding confluence of Quebrada LaTirana & Río Anorí, W slope, 7°18′N, 75°4′W, *Waide 62113* (UC); Mpio. San Carlos, corregimiento El Jordán, trocha Los Planes entre carr. alto de Samaná–Quebrada La Villa, Embalse de Punchiná, alrededores de Quebrada La Selva, *Velásquez & Zora 231* (UC); Mpio. San Luis, Piedra de Castillón, SW of town, ridge top leading to peak, 6°1′N, 75°1′W, *Daly & Betancur 5344* (UC). **Valle:** Bajo Calima, 15 km N of Buenaventura, Cartón de Colombia concession, 3°56′N, 77°8′W, *Gentry & Juncosa 40481* (MO, UC); same previous locality, *Gentry et al. 53667* (UC); Puerto Marizalde, Río Nanay, forest behind town, mostly *Campnosperma* Thwaites swamp, 3°15′N, 77°28′W, *Gentry & Juncosa 40565* (UC).

5. Peristethium confertiflorum Kuijt, sp. nov. TYPE: Peru. Cajamarca: San Ignacio, Distr. San José de Lourdes, Poblado Los Llanos, 5°5′33″S, 78°50′22″W, 2002 m, 16 Oct. 2006, *J. Perea & V. Flores 2902* (holotype, UC!; isotypes, AMAZ not seen, HUT not seen, MO not seen, MOL not seen, USM not seen). Figures 7, 8.

Haec species quoad folia ovato-elliptica basi truncata *Peristethio palandensi* Kuijt similis, sed ab eo habitu robusto, internodiis teretibus lenticellis parvis numerosis notatis atque inflorescentia congesta ex triadibus pluribus monadibus paucis ac pentadibus nonnullis constante distinguitur.

Plants presumed dioecious, the type female; stems stout, glabrous, internodes straight, terete, 8–10 cm, 8 mm thick where bearing inflorescences. Leaves to 16 × 8 cm, ovate-elliptic, apex acuminate, base truncate, venation pinnate, midrib reaching apex and strongly raised on abaxial surface; petiole 2 cm. Inflorescence axis lacking lenticels, 6–8 cm; ca. 24 pairs of crowded, somewhat deflected triads and 1 or 2 pairs of subterminal monads and a terminal flower; pairs of pentads present in mid-region of the inflorescence; peduncle ca. 5 mm. Flowers presumed bisexual, hexamerous, flower bud blunt-tipped. Male flowers with anthers 0.5 mm, sessile, placed at 2 different heights just below the tips of the petals; style 3 mm, stout, straight; stigma blunt, poorly differentiated. Female flowers 5 mm including the 1.5 × 1 mm ovary with finely denticulate calyculus. Fruit not known.

Distribution. *Peristethium confertiflorum* is only known from the type specimen collected at 2000 m from Cajamarca in Peru.

IUCN Red List category. The conservation status of the new species is Data Deficient (DD) (IUCN, 2001).

Discussion. The close geographic proximity and similarity in leaf shape might suggest that *Peristethium palandense* and *P. confertiflorum* are conspecific, but fundamental differences exist between the two species. *Peristethium confertiflorum* is an unusually stout plant with terete internodes bearing numerous, small lenticels, while stems of *P. palandense* are not at all stout (< 5 mm), and has somewhat quadrangular, smooth internodes. More significantly, the inflorescences of the two species are entirely distinct. *Peristethium confertiflorum* is characterized by numerous triads, with far fewer monads (one or two pairs) distal on a congested inflorescence, especially the tip being crowded. In *P. palandense*, the inflorescence is more open, with five to eight subterminal monad pairs and no terminal crowding. The occurrence of 5-flowered lateral units (pentads) on the inflorescence in *P. confertiflorum* is a unique feature (see below).

Unfortunately, the sexual condition of *Peristethium confertiflorum* remains uncertain. In the case of the type, the dimensions of the style seem to indicate fruit-producing capacity, but the anthers are of normal size and produce pollen. Its flowers may therefore be presumed as bisexual. The most extraordinary feature of the present species is the

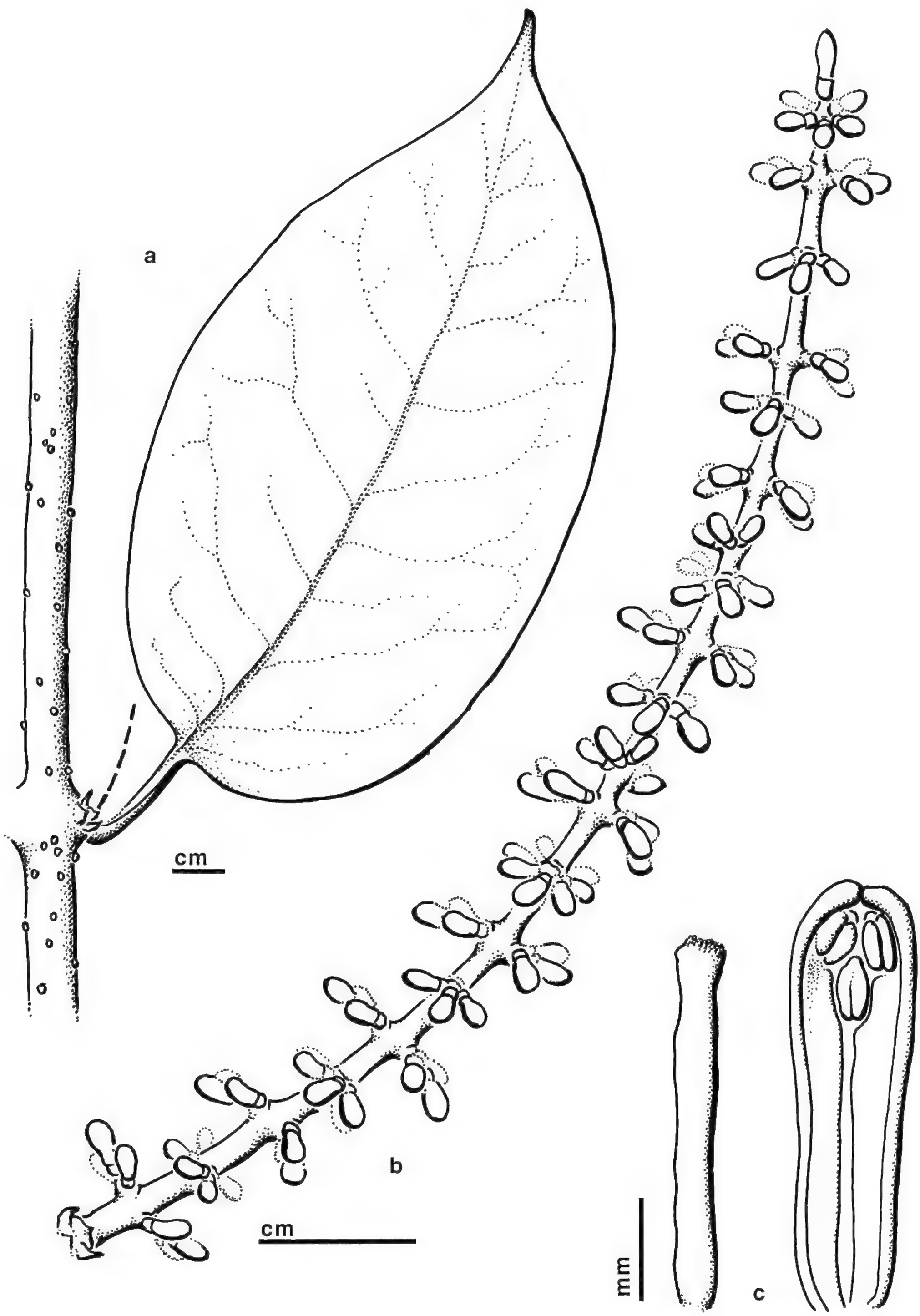

Figure 7. *Peristethium confertiflorum* Kuijt. —A. Leaf and adjacent stem, the broken line indicating the position of the inflorescence. —B. Inflorescence. —C. Floral dissection. Drawn from *Peres & Flores 2902* (UC). Scale bars: A, B = 1 cm; C = 1 mm.

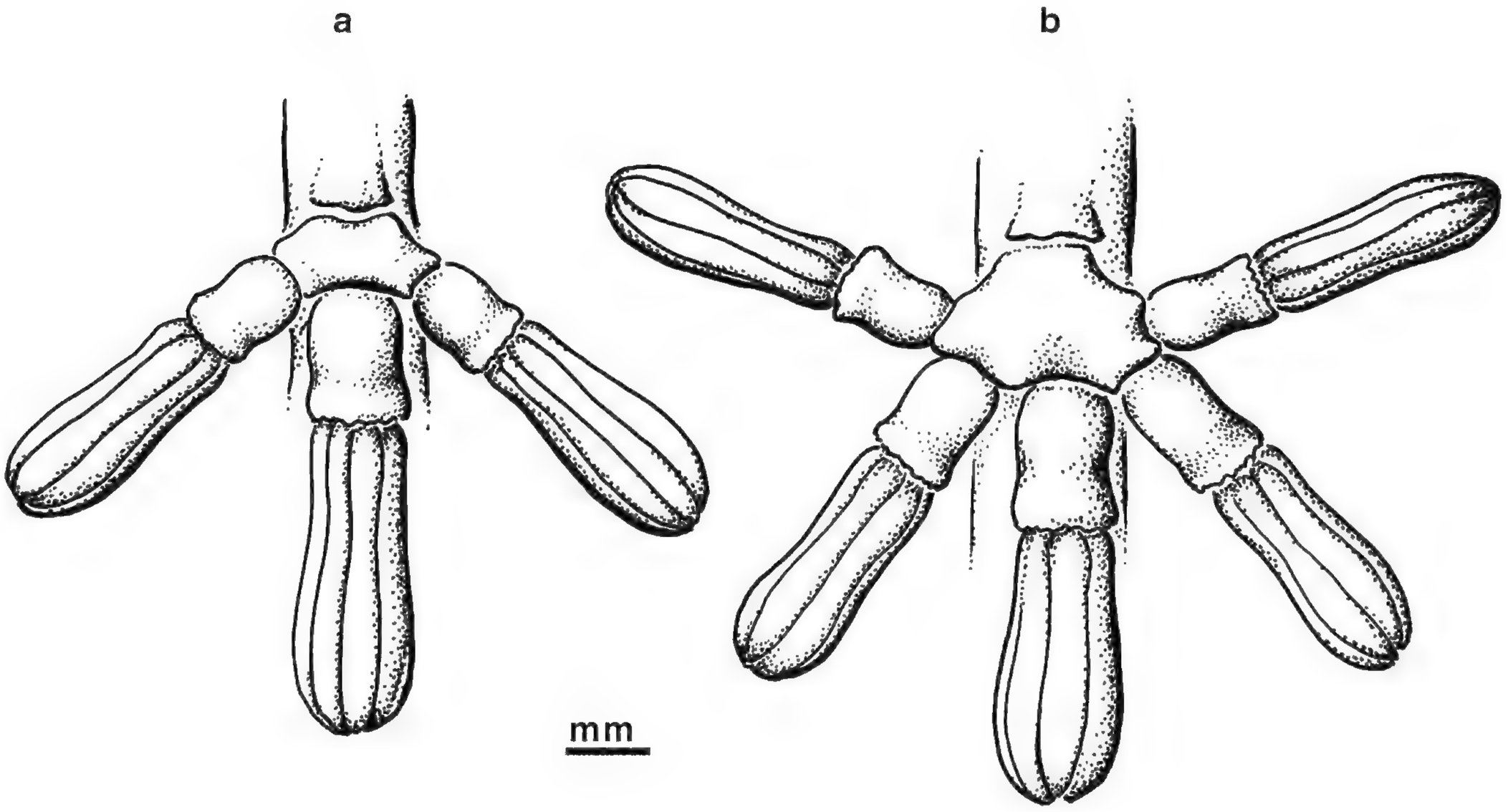

Figure 8. *Peristethium confertiflorum* Kuijt, lateral inflorescence units. —A. Triad. —B. Pentad. Drawn from *Peres & Flores 2902* (UC). Scale bars = 1 mm.

occurrence, usually in the mid-region of the inflorescence, of lateral units that are not triads but pentads, bearing five flowers in a somewhat fan-shaped, deflected configuration (Fig. 8). The peduncles of triads and pentads are scarcely recognizable, but are stout structures ca. 1 × 2 mm. The flowers are placed on this transverse, barlike structure that is placed more or less directly on the inflorescence axis. Most triads and pentads are somewhat deflexed, making it virtually impossible to discern the scar of the subtending bract. As it is, on these lateral units there seems to be no evidence of bracteole-like structures, although these may have fallen very early. Above each unit, the inflorescence axis shows a slightly overhanging, ridgelike lip. The median flower is the largest (and/or oldest) one, flanked on each side by two smaller (and/or younger) ones, all five of the flowers being more or less in the same plane. Having surveyed inflorescence structure of the family generally some years ago (Kuijt, 1981b), I can state that no comparable inflorescence structure is known elsewhere in Loranthaceae. The very rare pentads reported from *Passovia pyrifolia* (Kunth) Tiegh. are of an entirely different structure (Kuijt & Weberling, 1972).

6. Peristethium lamprophyllum Kuijt, sp. nov. TYPE: Colombia. Choco: area of Baudó, lt. side of Río Baudó, 7 km upstream from estuary, on shore opposite Quebrada Caimanerita, 11 Feb.–29 Mar. 1967, (♂ fl.), *H. P. Fuchs & L. Zanella 22060* (holotype, K!; isotypes, F!, US not seen). Figure 9.

Haec species quoad inflorescentiam triades floresque sessiles gerentem, flores hexameros etiam stylum rectum *Peristethio colombiano* Kuijt, *P. leptostachyo* (Kunth) Tiegh. et *P. lojae* (Kuijt) Kuijt similis, sed ab eis internodiis caulium floriferorum crassis, tumoribus gongylodibus ad axillas foliares prolificantibus, foliis adaxialiter nitidissimis atque inflorescentia axe elenticellato flore terminali ac monadibus subterminalibus ut videtur carente distinguitur.

Plants dioecious; stem internodes to 6 cm long and 1 cm thick when leaf-bearing, terete, with conspicuous knoblike, proliferating swellings in axils, with numerous small, pustular lenticels, to 6 cm and 1 cm thick. Leaves to 15 × 6 cm, ovate-lanceolate, very shiny above, dull below, apex acute, base obtuse, midvein strongly raised abaxially and grooved adaxially, running into apex, venation pinnate, with numerous lateral, oblique veins, much of the minor venation evident abaxially; distinct stout petiole, 1.5 cm. Male inflorescence axis somewhat keeled, smooth, without lenticels, with nodes not swollen, to 7 cm; 11 pairs of sessile triads, upper 1 or 2 nodes bearing possibly subterminal monads and terminal flower uncertain; basal inflorescence bracts several pairs, whitish, ovate-deltoid, 2 × 2 mm, apex acute; peduncle ca. 3 mm. Flowers hexamerous, flower buds 5 mm; petals essentially isomorphic; anthers 0.75 mm, sessile at 2 different heights near the petal tips; style 4 mm, slender, straight, stigma weakly developed; ovary 1 mm, apex rounded, calyculus

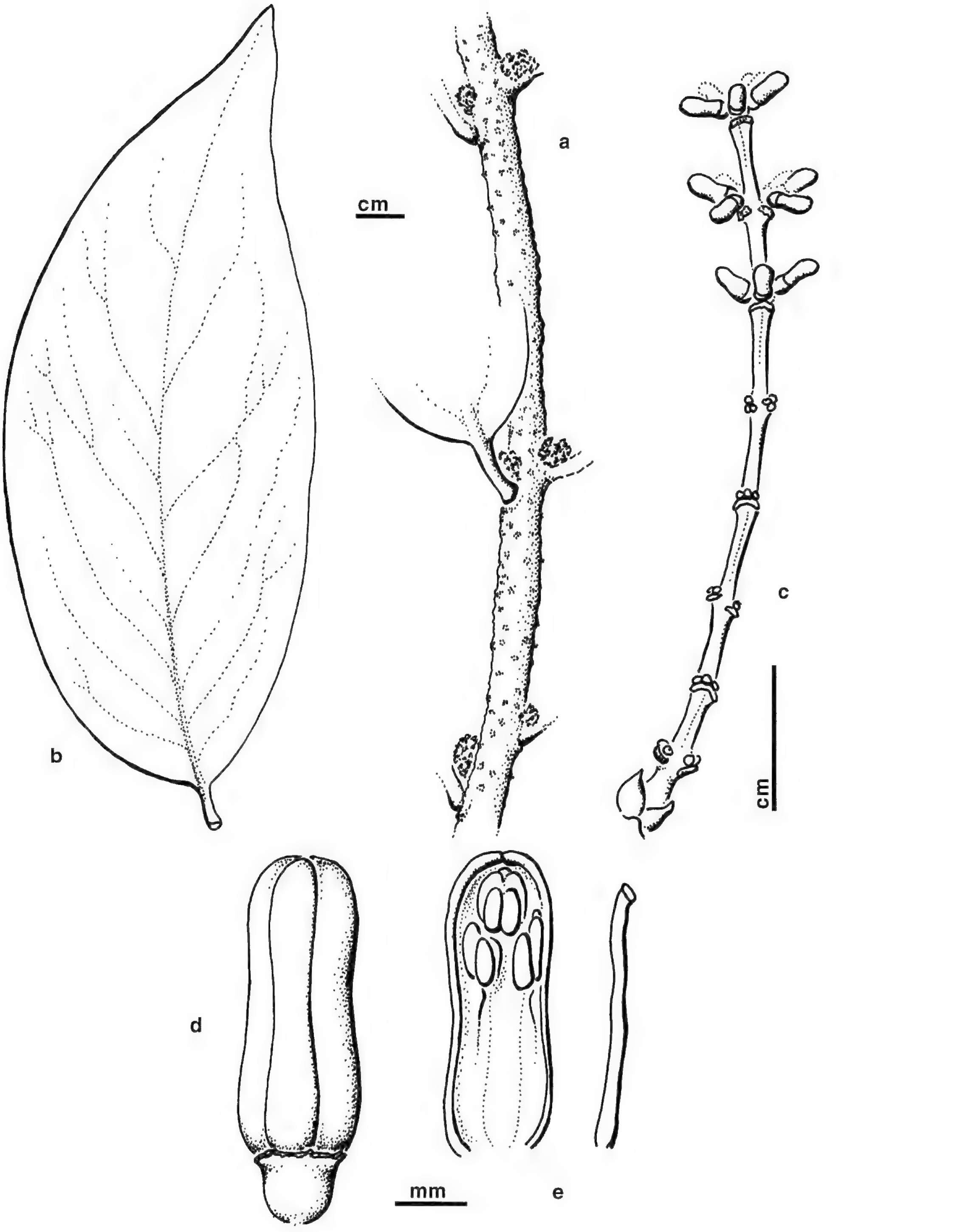

Figure 9. *Peristethium lamprophyllum* Kuijt. —A. Leaf-bearing stem, showing axillary knobs. —B. Leaf. —C. Inflorescence. —D, E. Mature flower bud and floral dissection. Drawn from *Fuchs & Zanella 22060* (K). Scale bars: A–C = 1 cm; D, E = 1 mm.

with minutely erose, darkened rim; pollen sacs 4, elongated, connectival horns very small or absent. Fruit not known.

Distribution. *Peristethium lamprophyllum* is only known from the type collection collected in Choco, Colombia.

IUCN Red List category. The conservation status of the new species is Data Deficient (DD) (IUCN, 2001).

Discussion. *Peristethium lamprophyllum* undoubtedly is an unrecognized species, even though the available material is sparse and badly fragmented. The stems are extremely stout, to 1 cm in diam., the leaves being strikingly shiny adaxially. The massive axillary knobs are made of numerous inflorescence scars; bract remnants are also very different from the other species here treated in which bracts are often caduous. The new species is similar to *P. leptostachyum*, which has matte leaves lacking the adaxial luster characteristic of *P. lamprophyllum* and does not develop the knoblike growths in the leaf axils. Unfortunately, the fragmented condition of the type of *P. lamprophyllum* denies me the possibility of ascertaining the construction of the inflorescence tip.

7. Peristethium leptostachyum (Kunth) Tiegh., Bull. Soc. Bot. France 42: 175. 1895. Basionym: *Loranthus leptostachyus* Kunth, Nov. Gen. Sp. [H.B.K.] (quarto ed.) 3: 440. 1818 [1820]. *Struthanthus leptostachyus* (Kunth) G. Don, Gen. Hist. 3: 411. 1834. TYPE: Colombia. "Crescit in andibus Quinduensium, inter Carthago et Buga, alt. 1200 hex. Floret Augusto," *Humboldt & Bonpland s.n.* (holotype, P!, P at F neg. 39627!; isotype, B†, B† at F neg. 11806!). Figure 10.

Loranthus pyrifolius Willd. ex Schult. f. in Schultes & Schultes, Syst. Veg., ed. 15 bis [Roemer & Schultes] 7: 1647. 1830, syn. nov., nom. illeg. superfl., non *Loranthus pyrifolius* Kunth, Nov. Gen. Sp. [H.B.K.] (quarto ed.) 3: 441. 1818 [1820]. TYPE: s. coll. (B-W 06975-010!).

Phthirusa pittieri K. Krause, Repert. Spec. Nov. Regni Veg. 15: 441–442. 1919, as "Pittieri." TYPE: Panama. Colón: "längs des Rïo Fato in Wäldern und Dickichten, um 10–100 m, als Parasit auf Sloanea-Arten," July–Aug. 1911, *H. Pittier 3911* (holotype, B†).

Plants dioecious, large, sparsely branched, the stout branches sometimes reaching several meters in length, 8 mm diam.; stem terete to somewhat ridged when young, bearing numerous pustular, cinnamon-brown lenticels; epicortical roots numerous, long, on stems and base of the plant. Leaves to 18 × 7 cm (rarely to 25 × 10 cm), broadly to narrowly lanceolate to ovate, somewhat thicker and rigid and usually pale green, apex attenuate, sometimes abruptly so, base mostly obtuse to truncate; petiole ca. 1 cm, strongly canaliculate. Inflorescence 1 to more per leaf axil, to 12 cm; with several sterile internodes and at least minute cinnamon-brown lenticels, with 12 or fewer numerous pairs of sessile triads and 1 or 2 pairs of single, sessile, ebracteolate monads and a single terminal flower, monads and triads not sunken in nodal cups; each inflorescence subtended by numerous pairs of chaffy, pale, usually early caducous bracts; floral bracts and bracteoles caducous; peduncle 2 cm. Flowers hexamerous, unisexual, not sunken in nodal cups, buds 4–5 mm; the female flower slender, the male flower clavate; anthers in the male flowers sessile, sometimes with twisted, white hairs directly below, in 2 series at slightly different heights above the middle of the petals; anthers in the female flowers sterile, straplike; stigma capitate, distinct, oblique; style essentially straight, present also in the male flower. Fruit to 7 × 5 mm, ellipsoid, dull brick red becoming waxy dark blue; seeds with endosperm hexagonal in section, embryo with poorly developed, slender haustorial pole.

Distribution. Collections of *Peristethium leptostachyum* have been seen from Costa Rica and Panama in Central America, and from Colombia, Ecuador, Peru, and Venezuela in South America. The taxon was collected at elevations ranging from sea level to 2370 m.

Discussion. The two collections from Peru below represent the first authentic records of *Peristethium leptostachyum* for Peru; both, however, are within a few kilometers from the Ecuadorian border.

The distinction between *Peristethium leptostachyum* and *P. polystachyum* is not directly obvious, and the two species have frequently been confused (as in Kuijt, 1964, where both species were included within *Struthanthus*); however, there are several clear differences. *Peristethium leptostachyum* has styles in all flowers, whatever sex; the species has cinnamon-brown lenticels on either the stem or the inflorescence axis (most commonly both, although the lenticels sometimes are minute); and its mature inflorescence nodes are not especially expanded even in fruit. Additionally, the leaves of *P. leptostachyum* tend to be thicker, mostly with a less attenuate apex, than those of *P. polystachyum*, which tend to be thin and markedly attenuate. The male flowers of *P. polystachyum* lack any vestige of a style, showing a small central cushion with a slight depression in its place; usually neither the stem internodes nor

Figure 10. *Peristethium leptostachyum* (Kunth) Tiegh. —A. Habit. —B, C. Male and female flowers, respectively. —D. Mature fruit. —E. Inflorescence (probably male) in earliest stage of expansion. A and D redrawn from Kuijt (1986), with permission from the author; B and C redrawn from Kuijt (1964), with permission from Bot. Jahrb. Syst., <http://www.schweizerbart.de>; E drawn from *Pérez et al. 255* (UC). Scale bar for B, C, and E applies to D. Scale bars: A = 1 cm; B–E = 1 mm.

inflorescence axis of either sex bear lenticels. The upper style of the female flower in *P. polystachyum* usually has a sigmoid shape in its upper half; the nodes of especially the infructescences are strongly expanded, and the flowers are inserted in conspicuous axial cups. Finally, the geographical range of *P. leptostachyum* reaches from northern Peru (Piura) and Ecuador to Costa Rica, while *P. polystachyum* is limited to north-central Peru except for two known nearby Bolivian collections (La Paz, Pando). There may be some possible geographical overlap between the two species.

The difference between male and female flowers is so slight that it is understandable that some earlier workers thought *Peristethium leptostachyum* had bisexual flowers. In fact, the species is dioecious, even though the male flower has a prominent style, while the female flower bears recognizable, strap-shaped or arrowshaped, sterile anthers.

The protologue of *Loranthus leptostachyus* speaks of monads ("Flores solitarii"), but this is probably an error and cannot be confirmed from the two type photographs available at the Field Museum. *Peristethium archeri* is the only known Colombian *Peristethium* species with purely monadic inflorescences and does not resemble the above two photographs, differing from *P. leptostachyum* also in being much smaller (leaves 3–10 × 2–5 cm) and having tetramerous, bisexual flowers.

Additional specimens examined. COLOMBIA. **Antioquia:** Medellín, grounds of the Facultad de Agronomía, on *Inga* Mill., *Cuatrecasas 24282* (US). **Magdalena:** Alto Río Buritaca, Alto de Mira, por el camino a la Cascada del Río Negro hasta la finca de Merardo, 11°5′N, 73°48′W, *Madriñán & Barbosa 267* (F). COSTA RICA. **Alajuela:** Cinchona, E of Vara Blanca de Sarapiquí, on *Eucalyptus* L'Hér., *Kuijt 2565* (CR, UBC); Canton San Carlos, Villa Quesada, *Smith 2583* (GH, MICH); region of Zarcero, Zapote de San Carlos, *Smith s.n.* (MO); Collines de San Ramon, *Tonduz 17733* (CR); entre Río Jesús y El Alto de Ramón, *Brenes 17134* (CR). **Puntarenas:** vic. of Palmar N, along Río Terraba, *Allen 5312* (UC, US); Golfito, *Kuijt 2558* (CR, UBC). **San José:** forest along Río Paquita, *Dodge & Goerger 9761* (F), *Dodge & Goerger 9762* (F, GH, MO); San Isidro del General, on *Pithecellobium longifolium* (Humb. & Bonpl. ex Willd.) Standl., *Kuijt 2445* (CR, UBC); vic. of El General, *Skutch 4023* (GH, MO, NY, US), *Skutch 4879* (GH, MO, NY, US), *Skutch 2618* (GH, MICH, MO, NY, US); La Hondura, *Standley 36236* (US), *Standley 37950* (US); near Quebradillas, 7 km N of Santa María de Dota, *Standley 42989* (US); S of Cartago, *Stork 416* (US); forêts du Copey, *Tonduz 11669* (CR, GH, NY, US). ECUADOR. **El Oro:** Km. 11 Atahualpa, Paccha, 03°33′05″S, 79°41′01″W, *Vargas et al. 5501* (MO, UC). **Imbabura:** Cotocachi, Parroquia García Moreno, Reserva Biológico Los Cedros, Sendero El Inca, 0°18′47″N, 78°46′27″W, *Vargas et al. 6525* (MO, UC). **Manabi:** Bosque Protector Cerro Pata de Pájaro, 15 km SE of Pedernales, 0°2′N, 79°57′W, *Neill et al. 11315* (MO, UC). **Zamora-Chinchipe:** Yacuambi, Centro Shuar Kurinta, Cordillera Kunku Naint (Cordillera de la Ciudad), Reserva Tukupi Nunke, *Cajekai et al. 782* (UC). PANAMA. **Coclé:** El Valle de Antón, *Allen 3721* (US). **Veraguas:** vic. Santa Fe, Cerro Tute, *Allen 4391* (K). PERU. **Piura:** Montaña de Cuyas, 10 km NE of Ayábaca, 4°32′S, 79°44′W, *Gentry et al. 75113* (MO). **Tumbes:** Prov. Zarumilla, carr. entre El Caucho y quebrada Naranjal, *Díaz et al. 7509* (MO). VENEZUELA. **Mérida:** Cerra de La Cuchilla, near Zea, *Velasco & Ramia 374* (VEN); above Hacienda Agua Blanca, above La Azulita, *Steyermark 56088* (F, US, VEN).

8. Peristethium lojae (Kuijt) Kuijt, comb. nov. Basionym: *Struthanthus lojae* Kuijt, Brittonia 32(4): 526–527, figs. 12–15. 1980. TYPE: Ecuador. Loja: 15 km S of Loja, 2600 m, *G. W. Harling 5808* (holotype, S!). Figure 11.

Plants robust, with regular, decussate phyllotaxy; stem internodes mostly 0.5 cm thick or less, straight, 4-angled, rather dark in color, with scattered, large lenticels; adventitious roots occasionally from stem nodes. Leaves 10 × 5 cm, somewhat coriaceous, lanceolate, apex acute, base rounded to truncate; petiole ca. 15 mm, discrete. Inflorescences 1 per leaf axil, the young fertile axis smooth, with lenticels developing when in fruit; nodes swollen, gradually expanding from ca. 2 cm at anthesis, to 7–11 cm in fruit; with numerous pairs of triads, 1 or 2 pairs of subterminal, ebracteolate monads, and 1 terminal flower; each inflorescence subtended by several pairs of smooth, papery bracts, bracts and bracteoles caducous. Flowers 6.5–8 mm (2–3 mm immature in type), ca. 1/2 of which is ovary with smooth calyculus, not sunken in nodal cups; petals 6, dimorphic, dull to golden yellow; anthers essentially sessile, placed at 2 different heights; style 1 mm, ± straight; stigma stout, weakly differentiated. Fruit obovoid, light violet-red or orange when immature, probably becoming purplish blue, at least 8 mm and 6 mm thick, the calyculus inconspicuous.

Distribution. *Peristethium lojae* is only known from collections from Ecuador at elevations between 2500 and 2730 m.

Discussion. The floral features illustrating the protologue of *Struthanthus lojae* (Kuijt, 1980) are immature; in reality, the flowers are nearly twice as long as shown (as in *Lewis et al. 2531*).

The 1980 protologue states that *Struthanthus lojae* is dioecious, with figure 14 (Kuijt, 1980: 525, my present Fig. 11C) supposedly showing floral details of the female flower. In retrospect, I feel this may well be in error, the flower buds being immature, and that the illustration shows what may be fertile anthers that are as large as others in the genus; if anything, they

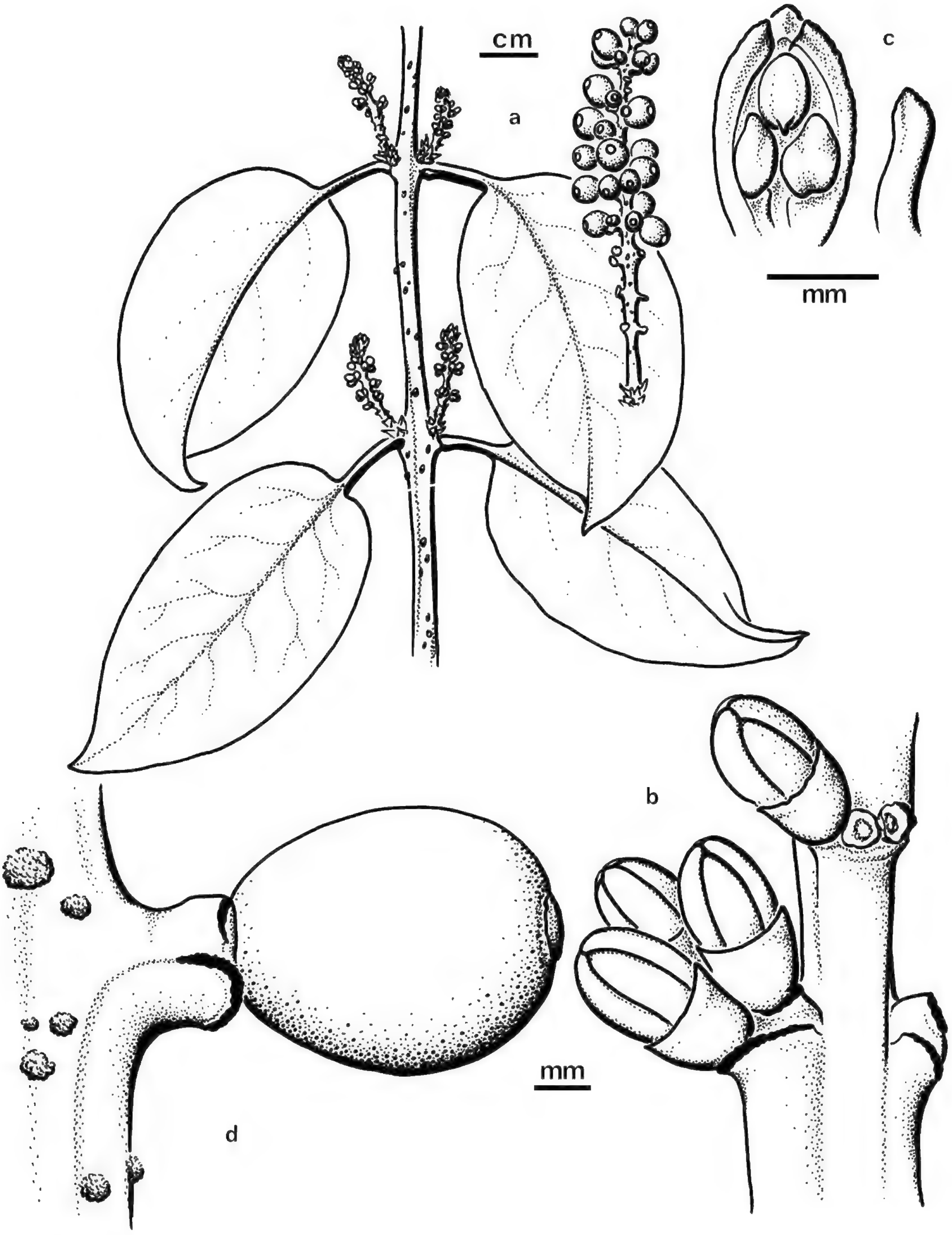

Figure 11. *Peristethium lojae* (Kuijt) Kuijt. —A. Habit and infructescence. —B. Portion of inflorescence. —C. Floral dissection. —D. Mature fruit (reprinted from Kuijt, 1986, with permission from the author). Scale bars: A = 1 cm; B–D = 1 mm.

are larger (6.5–8 mm). The closely related *Peristethium leptostachyum* is similar in general habit. In *P. leptostachyum*, however, the sterile anthers in the female flower are slender, straplike structures, in contrast to the epipetalous stamens inserted at two levels in *P. lojae*. Since the holotype bears fruit, it may be that *P. lojae*, in contrast to *P. leptostachyum*, has bisexual flowers.

Peristethium lojae is clearly different from *P. leptostachyum* and others: it is much stouter in all ways, with large clusters of persistent inflorescence bracts; flowers are 8 mm; drying dark (seen in all K specimens). The uncertainty expressed in my 1980 protologue of *Struthanthus lojae* as to its separation from *S. leptostachyus* has vanished in the face of its pollen morphology, which, especially in the presence of an apocolpium and in its diplocolpate structure, is completely distinct from that of *P. leptostachyum*.

Additional specimens examined. ECUADOR. **Loja:** track from Universidad Nac. Loja to Uritusinga, Km. 8, 4°2′S, 79°12′W, *Lewis et al. 2531* (K, UC); Km. 9.5, *Lewis et al. 3508* (K, UC); Km. 8 [4°2′S, 79°12′W], *Lewis et al. 2953* (K, UC).

9. Peristethium nitidum (Kuijt) Kuijt, comb. nov. Basionym: *Cladocolea nitida* Kuijt, Novon 13: 74–76. 2003. TYPE: Guyana. Potaro Siparuni Region: Pakaraima Mtns., Mt. Wokomung, ridgeline 0.5 km E of Wokomung escarpment adjacent Ka-Mie-Wah pinnacle, 5°4′N, 59°53′W, 1400–1500 m, 15 Nov. 1993, (♀ fls.), *T. W. Henkel, R. Williams, S. Fratello & P. Joseph 4400* (holotype, originally LEA, transferred to UC, UC-1954350!; isotype, US-03368714!). Figure 12.

Plants dioecious, the type female, sparsely branched, glabrous; stems quadrangular at least when young. Leaves regularly paired, to 5 × 2 cm, obovate, apex rounded to notched, sometimes nearly mucronulate, upper surface very shiny when dry, lower surface dull, venation pinnate, even the minor venation clearly marked; petiole ca. 1 cm, slender. Male plants not known. Female inflorescence 1 per axil, flanked by 2 acute prophylls becoming torn and corky with time, inflorescence including flowers 5–6 mm, determinate, consisting of 7 flowers in 3 decussate pairs and 1 terminal flower; all flowers ebracteolate, at least the lowest ones subtended by 1 caducous bract 2 mm, others apparently ebracteate. Flowers 4.5 mm of which 1 mm ovary with flaring, entire calyculus; petals 5, each with minute, elongate staminodial cushion; style nearly as long as the petals, surrounded basally by a nectary disk; stigma capitate, distinct, prominent, 0.75 mm wide. Fruit not known.

Distribution. *Peristethium nitidum* is known only from the type specimen, collected in Guyana.

Discussion. The caducous floral bracts, ebracteolate flowers, and minute, determinate inflorescences indicate a more appropriate placement of this rare species in *Peristethium*. It appears to be most closely related to *P. roraimense*, which has very similar inflorescences. Its pentamerous flowers are unique in small-flowered Loranthaceae.

10. Peristethium palandense Kuijt, sp. nov. TYPE: Ecuador. Zamora-Chinchipe: Palanda, cuenca del Río Chinchipe, sector de La Cruz, Palanda, 4°39′54″S, 79°4′56″W, 1840 m, 9 Mar. 2007, *W. Quizhpe & A. Wisum 2599* (holotype, UC!; isotypes, MO!, QCNE not seen). Figure 13.

Haec species quoad inflorescentiam triades monades floresque sessiles gerentem, flores hexameros etiam monades subterminales in paribus multis *Peristethio tortistylo* (Kuijt) Kuijt similis, sed ab eo internodiis quadrangularibus carinatisve atque inflorescentia longiore distinguitur.

Plants leggy, glabrous; internodes quadrangular to somewhat keeled, 6–7 cm, < 5 mm thick. Leaves to 14 × 5 cm, ovate-elliptic, apex cuspidate, base nearly truncate, venation pinnate, the midrib running into the apex and strongly raised on the abaxial surface; petiole 1.5–2 cm, discrete. Inflorescence axis somewhat terete, bearing sparse, yellowish brown, round lenticels, 8 or 9 pairs of well-spaced, sessile triads and 5 to 8 pairs of subterminal monads in open arrangement and 1 terminal flower; peduncles ca. 8 mm. Flowers sessile, presumed bisexual, hexamerous, not sunken in nodal cups, the nodes not expanded. Infructescence to 8.5 cm, subtended by caducous scales. Fruit ellipsoid-obovate, said to be black, truncate apically, 4 × 2.5 mm.

Distribution. *Peristethium paladense* is known only from the type collection from Ecuador, which was collected at 1840 m.

IUCN Red List category. The conservation status of *Peristethium palandense* is Data Deficient (DD) (IUCN, 2001).

Discussion. *Peristethium palandense* is distinguishable by its cuspidate leaf apices and long inflorescences, and especially the numerous monad pairs in their upper portion. The new species is known from the type collection only, bearing fruit, and regrettably, no flowers.

11. Peristethium peruviense (Kuijt) Kuijt, comb. nov. Basionym: *Cladocolea peruviensis* Kuijt, Novon 13: 76–77. 2003. TYPE: Peru. San Martín: Rioja–Pomacochas rd., below Venceremos, ca. 20 km NW of Rioja near Restaurant El Amigo, 05°45′S, 77°38′W, 1600 m, 8 Feb. 1984 (♀ fl.), *A. Gentry & D. N. Smith 45173* (holotype, MO-

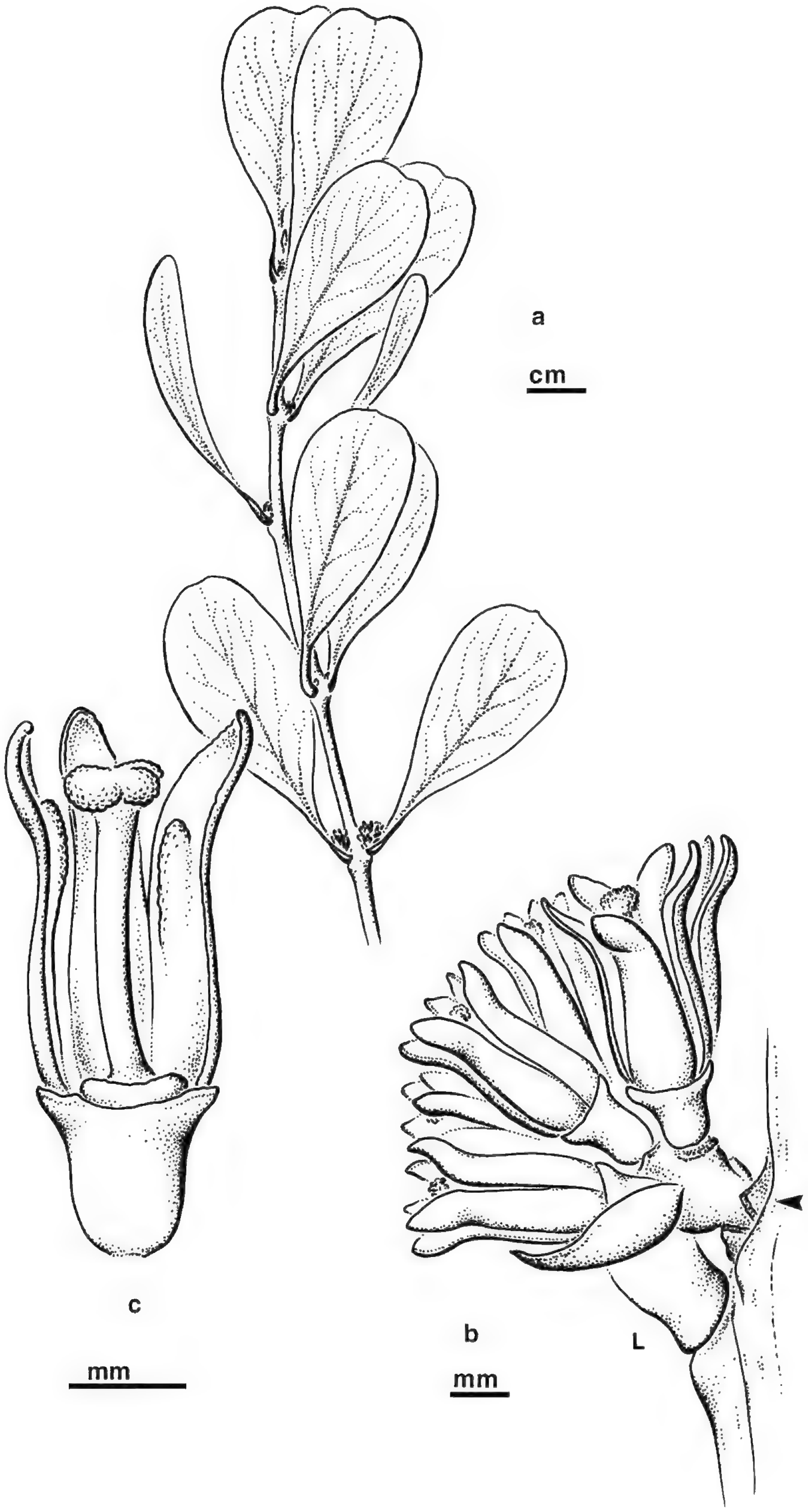

Figure 12. *Peristethium nitidum* (Kuijt) Kuijt. —A. Habit. —B. Female inflorescence. Five of the 7 flowers are visible, in the axil of a leaf (L); one floral bract is still in place, others have fallen. The arrowhead indicates a split, corky prophyll subtending the inflorescence. —C. Flower, the nearest two petals removed (reprinted from Kuijt, 2003a, with permission from Missouri Botanical Garden Press). Scale bars: A = 1 cm; B, C = 1 mm.

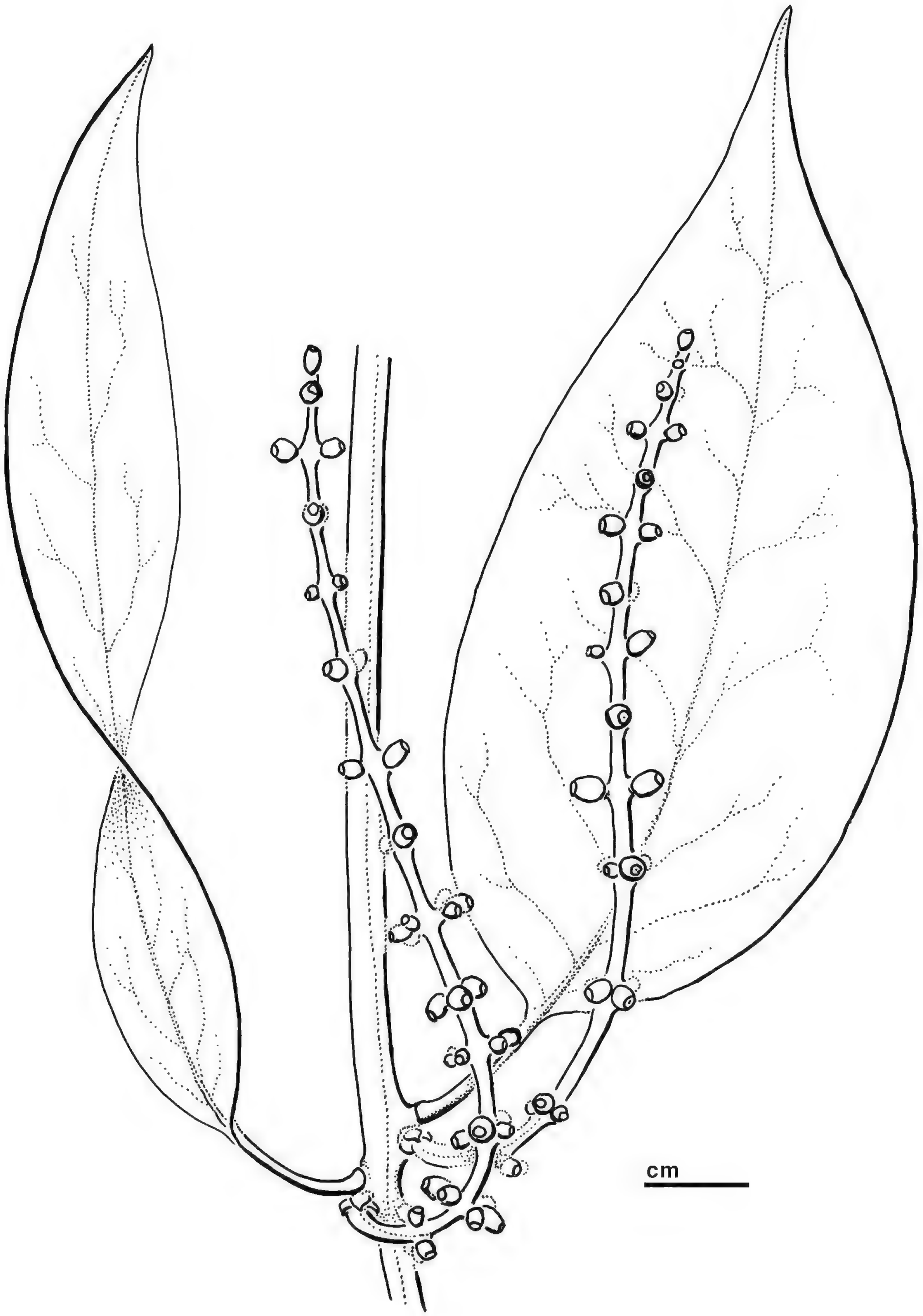

Figure 13. *Peristethium palandense* Kuijt, habit with young infructescences. Drawn from *Quizhpe & Wisum 2599* (UC). Scale bar = 1 cm.

4399772!; isotypes, originally LEA, transferred to UC, UC-1956802!). Figure 14.

Plants dioecious, only the type and female flowers known; stems probably dichotomous, innovations with 3 to 8 pairs of leaves, after which the apex apparently aborts; internodes somewhat angular or grooved, lacking lenticels when leaf-bearing, to 3 cm, older nodes somewhat swollen; phyllotaxy paired. Leaves to 10 × 5 cm, lanceolate to ovate, shiny above, dull below, apex obtuse to nearly acute, base tapering into indistinct, venation pinnate, evident, with numerous lateral veins; petiole 3–6 mm, flat. Male inflorescence 7–9 mm, on older growth and in leaf axils, subtended by several pairs of yellowish, chaffy bracts, the axis 5 mm; bearing 2 or 3(4) pairs of lateral, ebracteolate flowers and 1 terminal one, each with a pedicel ca. 0.6 mm, the subtending bracts small and caducous, inflorescence base surrounded by corky crater. Mature male flower bud 4.5 mm, slender; ovary 1 mm, calyculus nearly smooth; petals 4, 3.5 mm, strapshaped, scarcely dimorphic; petal with downward leading ridge below anthers; anthers 1 mm, sessile near the petal tips, at 2 slightly different heights, each 4-loculate, apex slightly notched; style lacking in male flower, center of flower with flat, papillate cushion slightly indented centrally. Fruit blue to purple.

Distribution. *Peristethium peruviense* is known only from six collections from Peru and two from southern Ecuador.

Discussion. The protologue already points out the surprising affinity to *Peristethium roraimense*.

Additional specimens examined. ECUADOR. **Zamora-Chinchipe:** area of Estación Científica San Francisco, 30 km on rd. Loja–Zamora, E of Ceja Andina, [3°58′18″S, 79°4′44″W], *Werner 1591* (UC); on Meliaceae, *Bussman et al. 12594* (MO). PERU. **Cajamarca:** San Ignacio, San José de Lourdes, 5°00′43″S, 78°54′9″W, *Campos & Vásquez 6405* (UC ex MO); base del Cerro Picorana, 04°59′25″S, 078°54′5″W, *Díaz et al. 10364* (UC ex MO); *10152* (F!-2255039).

12. Peristethium polystachyum (Ruiz & Pav.) Kuijt, comb. nov. Basionym: *Loranthus polystachyus* Ruiz & Pav., Fl. Peruv. [Ruiz & Pavon] 3: 50. 1802. *Struthanthus polystachyus* (Ruiz & Pav.) G. Don, Gen. Hist. 3: 410. 1834, non *Phthirusa polystachya* Eichler [= *Passovia stelis* (L.) Kuijt]. TYPE: Peru. s. loc., s.d., *Ruiz & Pavon s.n.* (holotype, MA not seen, MA at F photo neg. 29465!). Figure 15.

Plants dioecious, percurrent, glabrous; stems sparsely branched, lacking lenticels in the stems, branches to 2 m; internodes 3–8 cm, ± terete; epicortical roots unknown. Leaves paired, 7(–19) × 6(–7.5), apex acuminate to attenuate, base acute, tapering into the petiole, venation pinnate, evident, the midrib running into the apex; petiole 5–10 mm, slender, indistinct. Inflorescences several to many per leaf axil, to 6(10) cm, sometimes elongating to 12 cm, sometimes inflorescence axis with slender, linear lenticels to 5 mm (as in *Daly et al. 9901*, UC), the base with several pairs of blunt, caducous or eroding scale leaves, terminal flower, and to 3 pairs of subterminal monads in male plants, but conditions uncertain in female ones, triad pairs 10 to 13, the triad peduncle absent. Flowers hexamerous, attached directly to the inflorescence axis, in small cups. Male flower bud to 3.5–4 mm, clavate; the petal below with shoulder-like ridge; anthers nearly 1 mm, basifixed on short (< 0.5 mm) filament, nearly sessile, at 2 different heights, with small connectival horn; ovary 0.5 mm; style absent, the central cushion papillate, with small, central depression, rarely hairlike. Female flower with sigmoid style in upper 1/2 ca. 3 mm; stigma large, capitate; anthers inconspicuous sterile bulges. Fruit ovoid, blue, 6 mm and 3 mm thick, calyculus inconspicuous; fruit-bearing nodes greatly swollen.

Distribution. *Peristethium polystachyum* is found from northern Peru to Bolivia.

Discussion. *Peristethium polystachyum* is similar to *P. leptostachyum*, differing in the contorted style in the female flower and the absence (or near absence) of even a vestigial style in the male, and the knoblike expansion of at least the infructescence nodes, at each node appearing like six stout cupules (see type MA at F. neg. 19645). See also the comments under *P. leptostachyum* and *P. tortistylum*.

The collections *Janovec & Maceda 2721* (UC) and *Schunke V. 5816* (F) appear to have fruits, but in reality are male plants, the ovaries of which have become insect-galled; the same deceptive situation is occasionally seen in some Mexican *Struthanthus* species.

Boeke 2082 (UC), from Chachapoyas, Amazonas, Peru, is here provisionally listed under *Peristethium polystachyum* but lacks triadic knobs. It has unusually small flowers (petals 3 mm), isomorphic stamens, and an exceedingly slender, hairlike, straight style, but clearly is a male plant, having prominent anthers that occupy much of the flower (Fig. 15C). It may thus represent an unrecognized species.

The two collections from Venezuela cited in Rizzini (1982) belong to *Peristethium leptostachyum* instead (see under that species).

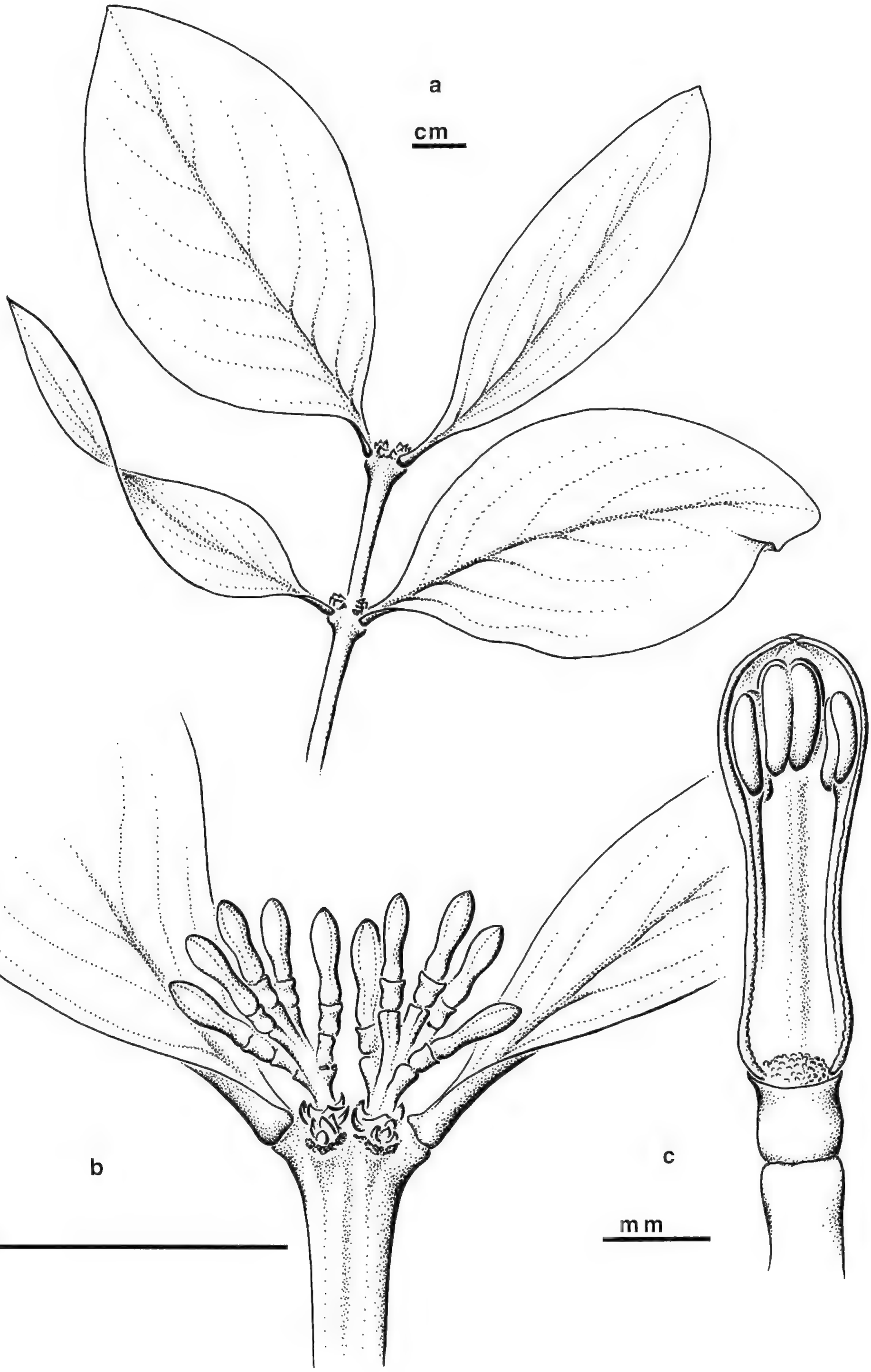

Figure 14. *Peristethium peruviense* (Kuijt) Kuijt. —A. Leafy, determinate shoot. —B. Two axillary inflorescences at the tip of part A. —C. Male flower, the nearest petal removed to show anthers, basal cushion, and absence of style (reprinted from Kuijt, 2003a, with permission from Missouri Botanical Garden Press). Scale bars: A, B = 1 cm; C = 1 mm.

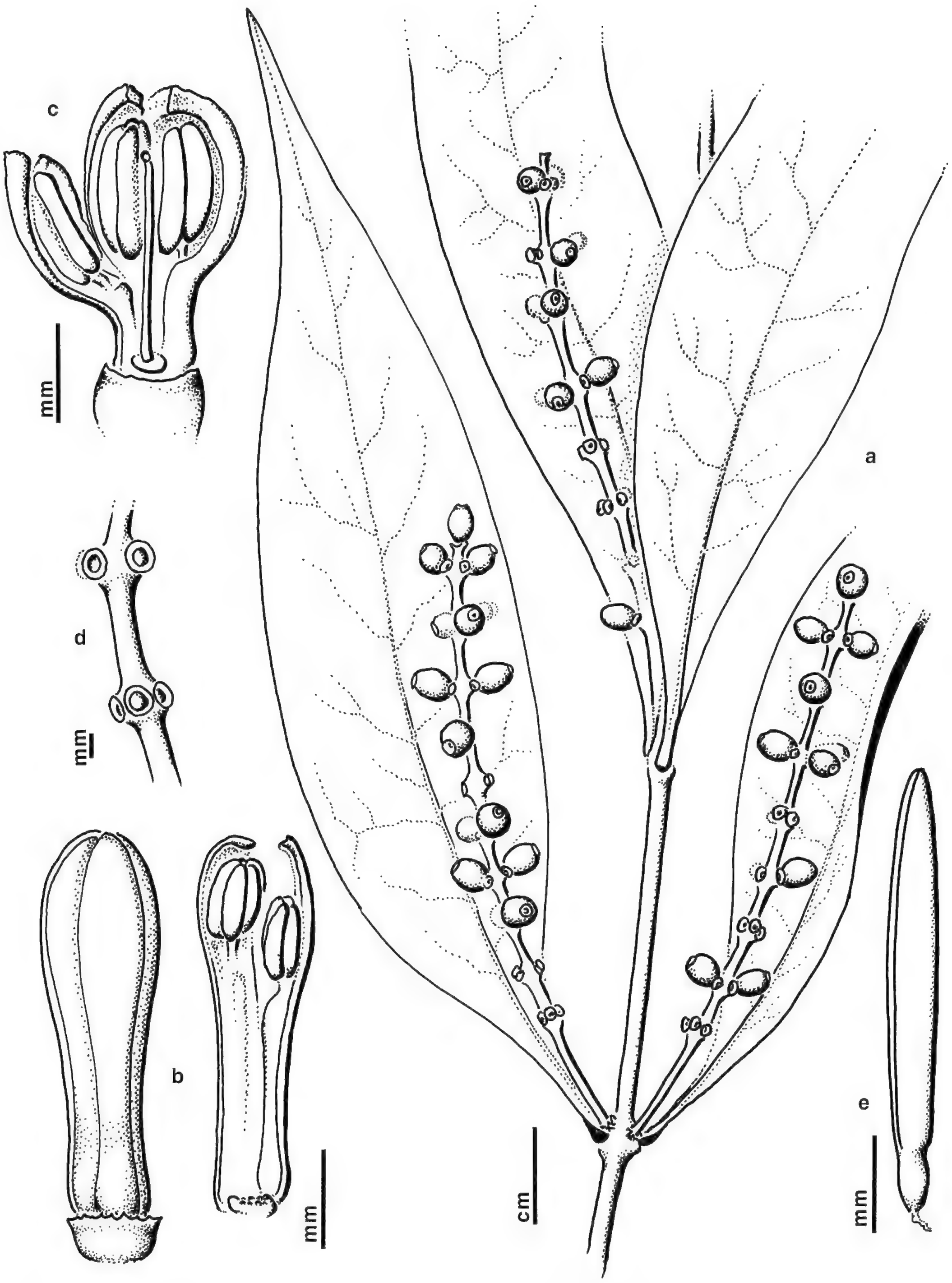

Figure 15. *Peristethium polystachyum* (Ruiz & Pav.) Kuijt. —A. Habit of fruiting plant. —B. Bud and floral dissection of male flower; note absence of style. —C. Floral dissection of male flower showing threadlike style. —D. Portion of old infructescence showing raised floral cups. —E. Embryo. A drawn from *Smith 1862* (UC). B drawn from *Foster 6166* (UC). C drawn from *Boeke 2082* (UC). D and E drawn from *Gentry et al. 70774* (UC). Scale bars: A = 1 cm; B–E = 1 mm.

A specimen from Loreto, Peru, is also tentatively placed here (*Klug 1562*, US). It is similar in appearance and has greatly contorted styles; additionally, the anther and supporting petals are comparable to those of other *Peristethium*. The inflorescence appears to consist of only two to three nodes, at least the basal ones triadic. However, all flowers are pedicellate (pedicels 0.5 mm), as are the triads, conditions that disagree with typical *P. polystachyum*. Unfortunately, the specimen does not yield further definitive characteristics.

Curiously, the female herbarium specimens of *Peristethium polystachyum* seem to greatly outnumber the male ones; at UC, there are only two male specimens, but 12 female ones.

Additional specimens examined. BOLIVIA. **La Paz:** Alto Madidi, rd. 3–5 km NE of camp, 13°35′S, 68°46′W, *Gentry et al. 70774* (UC ex MO). **Pando:** Nicolás Suárez, ca. de Cobija en las prox. del Aeropuerto, *Casas & Susanna 8096* (NY). PERU. **Amazonas:** Prov. Chachapoyas, Leimebamba–Chilcos trail, Chilcos, *Boeke 2082* (MO, NY). **Cajamarca:** San Ignacio, San José de Lourdes, base del Cerro Picorana, 4°59′25″S, 78°54′5″W, *Díaz et al. 10364* (UC); San Ignacio, San José de Lourdes, 5°0′43″S, *Campos & Vásquez 6405* (UC). **Huánuco:** Prov. Huánuco, Chinchao, Pampayacu, 1 km E of Cochero, *Schunke V. 5804* (F, NY); possibly in Huánuco, SW slope of Río Hualla Pichis watershed, ascent of Cerro del Sira, 9°25′S, 74°42′W, *Dudley 13450* (F); Prov. Leoncio Prado, Distr. Rupa Rupa, E of Tingo María, near Cerro Quemado, *J. Schunke V. 10615* (MO). **Loreto:** near Mishayacu, near Iquitos, *Klug 1562* (US). **Madre de Díos:** rd. to Tambopata, N of Puerto Maldonado, *Gentry et al. 19603* (F, MO); Tambopata, outskirts of Puerto Maldonado, 12°35′S, 69°10′W, *Gentry & Young 31769* (MO); Prov. Manu, Puerto Maldonado, Los Amigos Biological Station, Madre de Díos River, 7 km upriver from mouth of Río Los Amigos, on *Inga* Miller, *J. Schunke V. 5816* (F); *Janovec & Maceda 2721* (UC); Parque Nacional del Manu, Río Manu, Cocha Cashu Station, *Foster & Terborgh 6166* (MO). **Pasco:** Prov. Oxapampa, Palcazo Valley, Cabeza del Mono, 5–6 km W of Iscozacin (10°12′S, 17°14′W), *Smith 3819* (NY ex MO); Iscozacin, near confluence of Río Palcazu and Río Iscozacin, Juan Franzen property, 10°12′S, 75°13′W, on *Inga*, *Smith 1906* (NY); on *Citrus* L., *Smith 1862* (NY). **Piura:** Huancabamba, Prov. Canchaque, Chorro Blanco, *Díaz et al. 2751* (MO). **Puno:** Prov. Sandia, 12.5–13.8°S, betw. Río Azata & Colorado, on *Calliandra* Benth., *Núñez & Muños 5248* (F, MO). **Ucayali:** Prov. Purús, Distr. Purús, abajo del Pto. Esperanza, margen derecho del Río Purús, 10°12′S, 70°57′W, *Schunke-Vigo & Graham S14995* (NY).

13. Peristethium primarium (Kuijt) Kuijt, comb. nov. *Cladocolea primaria* Kuijt, Ann. Missouri Bot. Gard. 74: 511–514. 1987. TYPE: Panama. Panamá: Cerro Jefe, 2 km along rd. to Altos de Pacora from jct. with rd. to peak, low cloud forest, 800 m, 24 May 1981, *K. J. Sytsma & S. Knapp 4797* (holotype, MO-3404269!; isotypes, originally LEA, transferred to UC, UC-1956823!). Figures 16, 17.

Plants sparsely branched, twining, glabrous; stems terete or slightly 4-ridged, often with conspicuous lenticels when older, straight and rather rigid; epicortical roots occasionally present on the stems and probably from the base. Leaves paired, somewhat leathery, broadly lanceolate to ovate, apex mostly blunt or slightly apiculate, venation inconspicuous, midrib conspicuous and running into apex; petioles stout, 10–15 mm. Inflorescences subtended by several pairs of thick, brown scale leaves, solitary in leaf axils, determinate; with 3 or 4(5) pairs of triads, 2 pairs crowded at the base and a pair somewhat higher, followed by a pair of ebracteolate monads and a terminal flower, the basal triads crowded in the leaf axil. Flowers bisexual, pale yellow, 4-partite; petals slightly dimorphic, 2–2.5 mm; anthers very small, placed on upper part of petals, sessile on the shorter petals and with very short filaments on the longer ones; ovary 1.5 × 1 mm; style ± straight; stigma capitate, oblique, reaching the petal tips. Fruit ellipsoid, red, becoming dark purple, 6 × 4 mm; calyculus inconspicuous; embryo dicotylous, slender, the haustorial pole scarcely expanded.

Distribution. *Peristethium primarium* as described (Kuijt, 1987a) is restricted to the province of Panama, to the Cerro Jefe area; because of this, one disjunct collection is noted from Colón in Panama.

Discussion. The collection from Colón (*McPherson & Van der Werff 19998*, MO) represents a remarkable disjunction; all other known specimens have been gathered in the Cerro Jefe area. As far as I know, it represents the only known, convincing example of long-distance dispersal within a single landmass; other (very few) instances have been recorded only from pelagic islands, as *Phoradendron berteroanum* (DC.) Griseb. on the Galápagos Islands, *P. piperoides* (Kunth) Trel. on Cocos Island (Kuijt, 2003b), and *Dendropemon caymanensis* Proctor from Little Cayman Island (Kuijt, 2011a). The specimen has slightly larger leaves and internodes, the leaf apex being somewhat acuminate, but the structure of the inflorescence is identical to that of Cerro Jefe material.

Additional specimens examined. PANAMA. **Colón:** Teck Cominco Petaquilla mining concession, streamside forest by old Petaquilla camp, 8°50′14″N, 80°41′17″W, *McPherson & Van der Werff 19998* (MO). **Panamá:** forest near rd. to Cerro Jefe, near jct. with rd. to Altos de Pacora, *Mori & Kallunki 2763* (NY, UC); Cerro Jefe, 6.6 mi. above Goofy Lake, *Sytsma et al. 2839* (UC); near radio tower, *D'Arcy & Hamilton 14817* (UC); Cerro Jefe, 9°15′N,

Figure 16. *Peristethium primarium* (Kuijt) Kuijt, habit (reprinted from Kuijt, 1987a, with permission from Missouri Botanical Garden Press). Scale bar = 1 cm.

79°20′W, *Hamilton & D'Arcy 611* (UC). PERU. **Loreto:** near Mishayacu, near Iquitos, *Klug 1562* (US).

14. Peristethium roraimense (Steyerm.) Kuijt, comb. nov. Basionym: *Phthirusa roraimensis* Steyerm., Fieldiana, Bot. 28: 224, 225. 1951. *Cladocolea roraimensis* (Steyerm.) Kuijt, J. Arnold Arbor. 56: 326–327. 1975. TYPE: Venezuela. Bolívar: Mt. Roraima, SW-facing forested slopes betw. Rondón Camp & base of sandstone bluffs, 2040–2255 m, 30 Sept. 1944, *Steyermark 58943* (holotype, F-1284129!; isotypes, NY-285200!, US!). Figure 18.

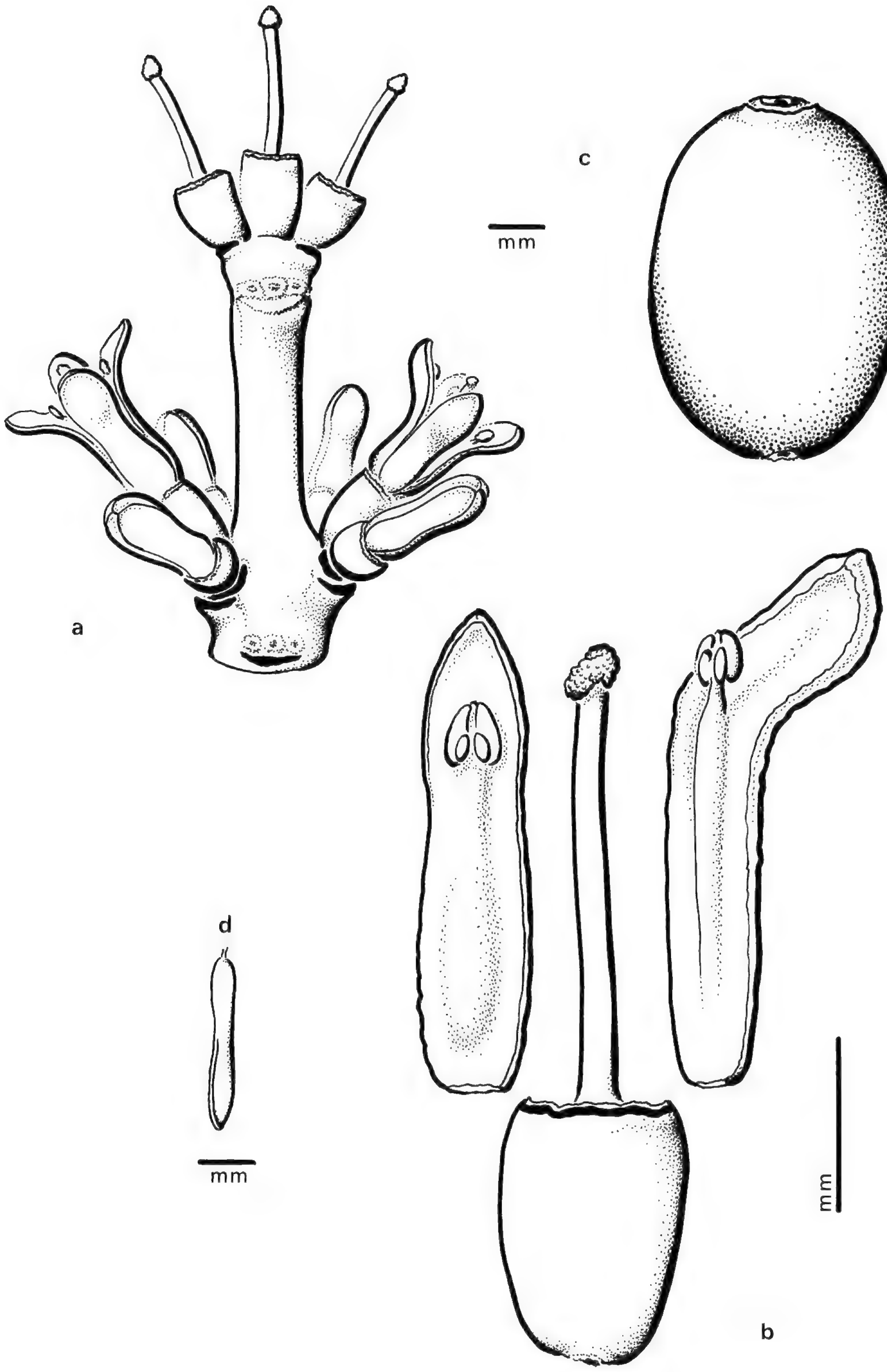

Figure 17. *Peristethium primarium* (Kuijt) Kuijt. —A. Inflorescence, the upper triads removed. —B. Floral dissection. —C. Mature fruit. —D. Embryo (reprinted from Kuijt, 1987a, with permission from Missouri Botanical Garden Press). Scale bars = 1 mm.

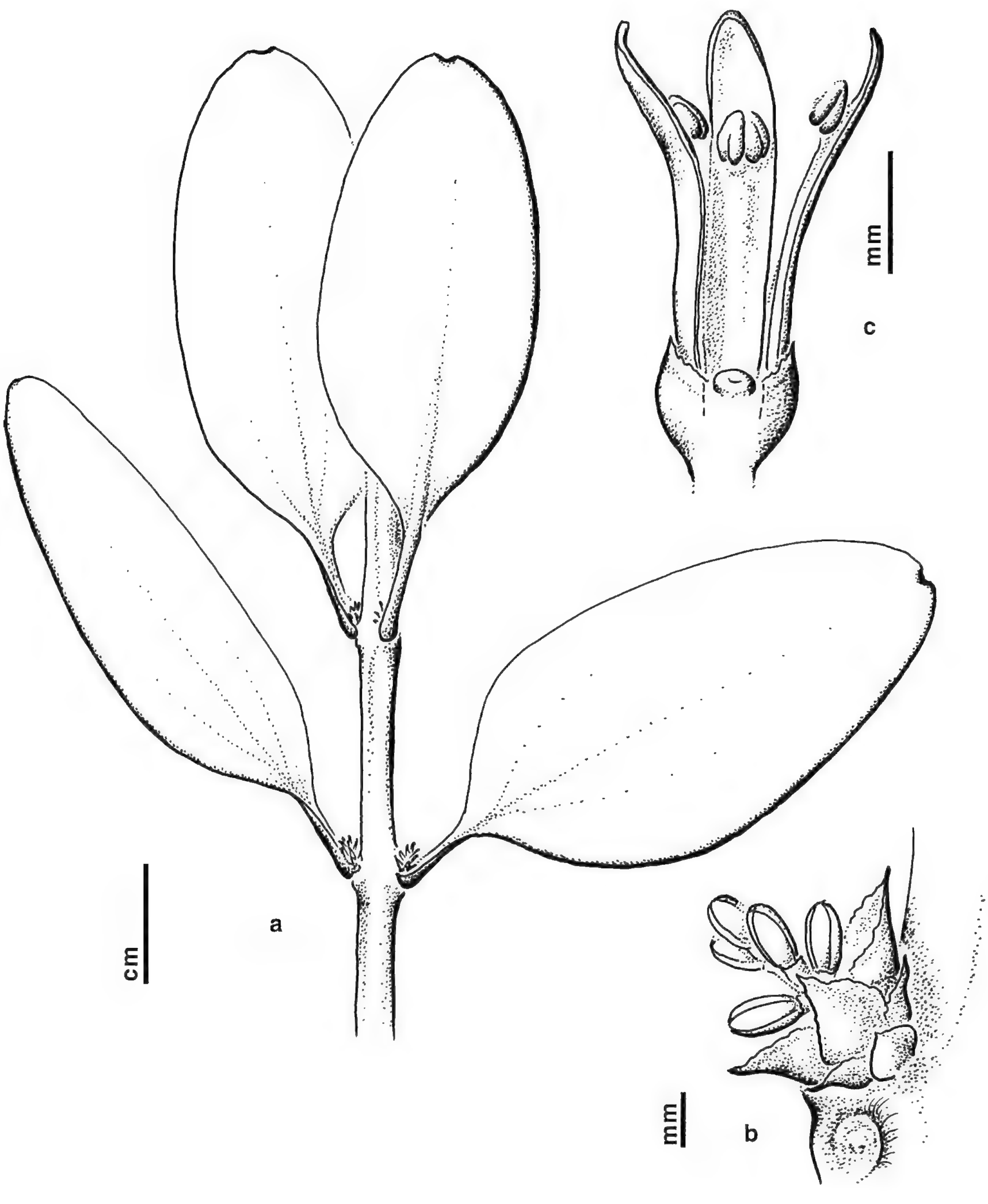

Figure 18. *Peristethium roraimense* (Steyerm.) Kuijt. —A. Habit, reconstructed. —B. Immature inflorescence above leaf scar. —C. Mature flower, the nearest petal removed to show the central cushion and absence of style (reprinted from Kuijt, 1975b, with permission from the author). Scale bars: A = 1 cm; B, C = 1 mm.

Plants rigid, percurrent; stems somewhat succulent, 2–5 mm thick, bark smooth; internodes rather short (1–3 cm); epicortical roots not seen. Leaves decussate, 40–50 × 10–25 mm, elliptic to ovate to obovate, olive-green to bronze, coriaceous, apex obtuse or more commonly emarginate through loss of a caducous, brown, nail-like tip 1 × 1 mm, base obtuse to acute, venation obscure; mesophyll differentiated into sclereids with many bulbous arms; petiole ca. 3 mm, strongly canaliculate. Inflorescence 1 per leaf axil, subtended by several pairs of acute, chartaceous bracts; 1–2 mm; flowers paired, sessile, ebracteolate monads and a single terminal flower; floral bracts caducous. Flowers 7 to 9 per inflores-

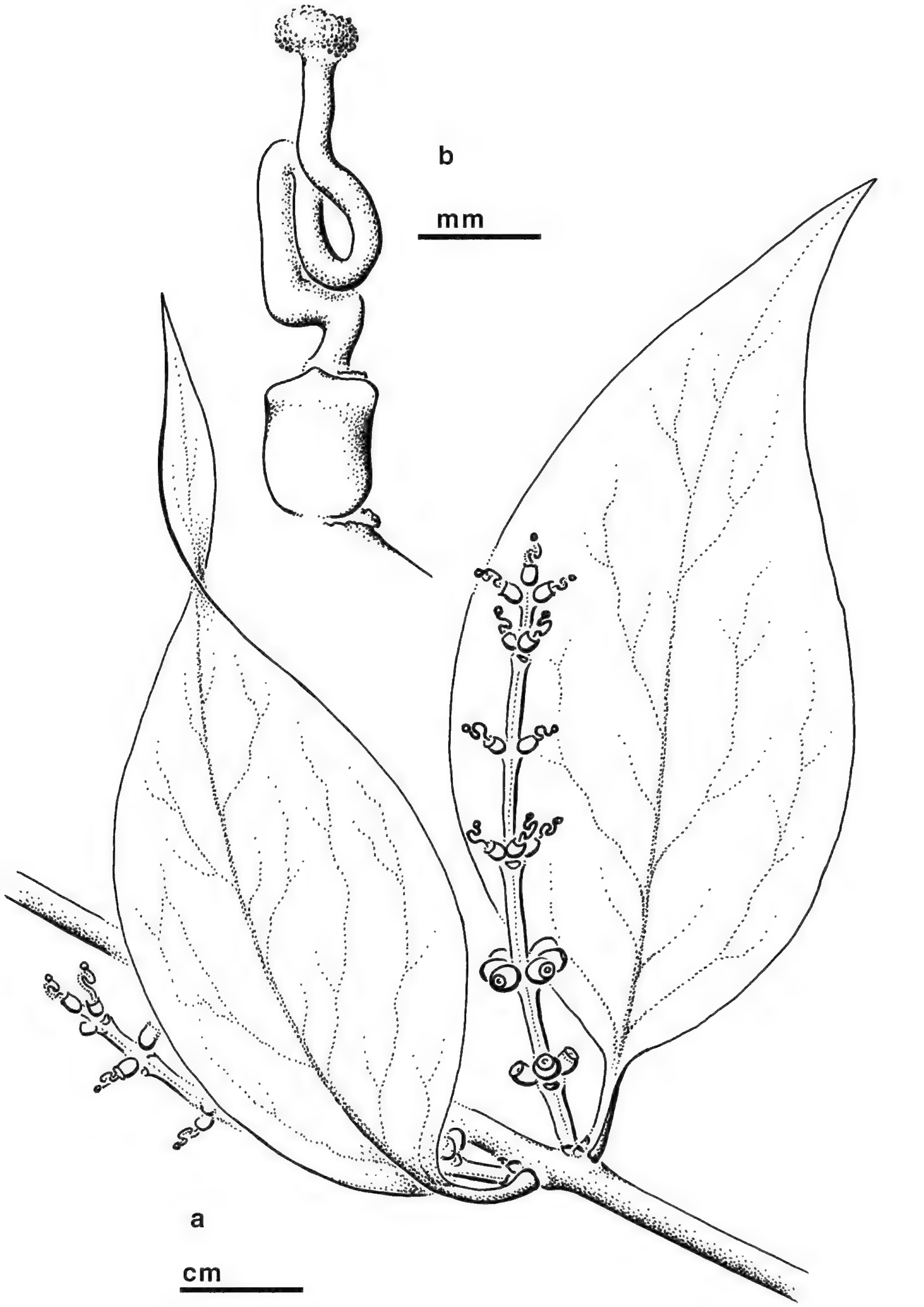

Figure 19. *Peristethium tortistylum* (Kuijt) Kuijt. —A. Habit of young fruiting plant. —B. Ovary and style (reprinted from Kuijt, 2003a, with permission from Missouri Botanical Garden Press). Scale bars: A = 1 cm; B = 1 mm.

cence, yellowish; calyculus prominently 2-dentate; petals 4, each 4 mm; with a sessile anther above the middle in biseriate arrangement; pollen smooth, round-triangular, with little or no evidence of triradiate grooves (colpi); style not seen. Fruit oblong-ovoid, said to be dull blue-green (*Steyermark 58943*), 7 × 5 mm, the fruiting axis elongating to ca. 12 mm.

Distribution. In Kuijt (1975b), only two collections of *Peristethium roraimense* are listed, both from exactly the same spot on Mt. Roraima.

Discussion. *Peristethium roraimense* is perhaps the rarest of all South American mistletoes and is characterized by an exceedingly small inflorescence that nevertheless corresponds in all structural details to that of other species, especially *P. peruviense*. In both species, a style appears to be completely lacking in male flowers. In the protologue, the species is stated to have 5- or 6-merous flowers, but that is in error, as the flowers, again like *P. peruviense* and others, are 4-merous.

Additional specimens examined. Location same as the type, *Steyermark 58965* (F, US).

15. Peristethium tortistylum (Kuijt) Kuijt, comb. nov. Basionym: *Struthanthus tortistylus* Kuijt, Novon 13: 82–83. 2003. TYPE: Ecuador. Pastaza: Kapawí (Amuntai), Río Pastaza, on pasture tree, 2°31′S, 76°48′W, 235 m, 14–20 July 1988, *W. H. Lewis, M. Elvin-Lewis, C. E. Cerón, E. J. Kenelly & M. C. Gnerre 13615* (holotype, MO-6323705!; isotype, UC!). Figure 19.

Plants possibly dioecious, robust, glabrous; stem internodes 3–8 cm, terete. Leaves to 10 × 4.5 cm, ovate, shiny when dry, apex attenuate, base obtuse, venation pinnate, even the minor venation evident, midvein running into apex, with 4 basal lateral veins running at least halfway down the blade; petiole 1 cm, distinct. Fruit-bearing inflorescence ca. 4 cm, subtended by 2 or more small, blunt, partly caducous scale leaves, axis angular; peduncle 4–6 mm, followed by ca. 4 pairs of triads and 1 to 3 pairs of monads and a single terminal flower; triads and flowers sessile, at least the lower bracts broad, with obtuse apex, caducous. Flowers hexamerous, not sunken in nodal cups, flower bud 3.5 mm; ovary ca. 1 mm; anthers extremely small, ovate, essentially sessile; style perhaps twice as long as the petals, tightly contorted even after anthesis; stigma large, capitate. Fruit (immature) ovoid, apex blunt, calyculus irregularly dentate.

Distribution. *Peristethium tortistylum* is so far known only from its type, collected in Ecuador (Pastaza).

Discussion. The protologue of *Struthanthus tortistylus* (Kuijt, 2003a) described the plant as dioecious, but I now regard that as insufficiently established, and the possibility of bisexual flowers cannot be excluded. A single petal with a normal, minute anther has been observed on the UC isotype, suggesting bisexual flowers, but this aspect needs better documentation.

Peristethium tortistylum is morphologically similar to both *P. aequatoris* and *P. polystachyum*. From both latter taxa, *P. tortistylum* is distinguished by its one to several pairs of subterminal monads and an evident terminal flower that is raised on a short length of inflorescence axis, exceeding the sessile triads. From *P. aequatoris*, it differs in the fact that the branches are terete (vs. slightly quadrangular to carinate). *Peristethium polystachyum*, being dioecious, has twisted styles in its female flowers, and male flowers generally have no styles; another difference is the crowded condition of its most distal flowers, where a pair of monads is rarely found. Once plants of *P. polystachyum* develop fruits, the most striking characteristic of that species is the dramatic swelling of the inflorescence nodes, giving the axis a somewhat beaded aspect, the fruits placed in nodal cups. This aspect is clearly visible in the type photograph of *P. polystachyum* (F neg. 29465). *Peristethium tortistylum* does not exhibit this feature.

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A TAXONOMIC REVISION OF THE GENUS *PHYLA* (VERBENACEAE)[1]

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Abstract

A taxonomic revision of the genus *Phyla* Lour. is provided. *Phyla* is a small genus in Verbenaceae, placed in the tribe Lantaneae and represented by five species and three varieties. Four species are found only in the Americas, and one, *P. nodiflora* (L.) Greene, is found worldwide in tropical and temperate areas. Detailed morphological descriptions are given for each taxon, as well as a key for their identification, illustrations, synonymy, distribution, selected specimens, and discussion about the relationships among closely related taxa. *Cryptocalyx nepetifolia* Benth. is lectotypified, and one new combination is proposed, *P. nodiflora* var. *minor* (Hook.) N. O'Leary & Múlgura.

Key words: Americas, *Lippia*, *Phyla*, taxonomy, Verbenaceae.

Loureiro (1790) founded *Phyla* Lour. with a species from Cochinchina, Vietnam, which he named *P. chinensis* Lour. (a synonym of *P. nodiflora* (L.) Greene). *Phyla* belongs to tribe Lantaneae (Schauer) Briq., along with the closely related genera *Lippia* L., *Lantana* L., *Aloysia* Paláu, and others (Atkins, 2004). Many botanists have treated *Phyla* under *Lippia* (Schauer, 1847; Briquet, 1895; Macbride, 1960; Gibson, 1970; Jansen-Jacobs, 1988; Brako & Zarucchi, 1993; Sanders, 2001; Rzedowski & Rzedowski, 2002). However, both genera have been accepted as distinct by various authors (Greene, 1899; Moldenke, 1942, 1973a, 1983; Troncoso, 1965, 1979; Wiggins & Porter, 1971; López-Palacios, 1977; Wiggins, 1980; Munir, 1993; Troncoso & Botta, 1993; Jørgensen & León-Yánez, 1999; Pool, 2001; Méndez Santos, 2003; Múlgura, 2003; Atkins, 2004).

In the following treatment, five species under *Phyla* are recognized, with three infraspecific taxa for *P. nodiflora*. *Phyla*, with its prostrate herbaceous plants rooting at the nodes, malpighiaceous hairs, and generally uncinate hairs on the calyx, is distinguished from the closely related genus *Lippia*. In contrast, *Lippia* is defined as a taxon of spreading shrubs, with simple, non-malpighiaceous hairs and the absence of uncinate hairs on the calyx (Greene, 1899). In addition, phylogenetic studies (Marx et al., 2010) show *Phyla*, as circumscribed here, as a highly supported monophyletic group.

Materials and Methods

This taxonomic revision is based on herbarium collections from the following herbaria: BM, G, MO, NY, SI, and US. Flower measurements were taken from material rehydrated by boiling. Fruit measurements were taken from dried specimens. The descriptive terminology of the inflorescences used here is in accordance with Múlgura et al. (2002), the morphological terms follow Hickey (1974), and the description of pubescence corresponds to Lawrence (1951). We considered varietal status for taxa when we observed a group of organisms with a gradual variation of characters, which would suggest an incomplete segregation of two incipient species sharing the same geographical area, following Suttill and Allen (1992), who considered varieties when differences were morphological but not geographical. The distribution and habitat data of taxa were taken from herbarium specimen labels. Appendix 1 includes a list of accepted taxa and a complete list of examined specimens.

Taxonomic Treatment

I. Phyla Lour., Fl. Cochinch. 66. 1790. *Piarimula* Raf., Fl. Tellur. 2: 102. 1836, nom. illeg. TYPE: *Phyla chinensis* Lour. [= *Phyla nodiflora* (L.) Greene].

Pilopus Raf., Fl. Tellur. 2: 102. 1836 [1837], replacement name for *Bertolonia* Raf., Chloris Aetn. 5. 1815, nom.

[1] We thank the curators of the herbaria cited in the text for the loan of specimens and assistance in the search of type material, especially J. Mueller (JE), L. Gautier (G), A. Reznicek (MICH), L. Walsingham (K), R. Dominik and R. Vogt (B), and D. Trock (CAS). This study was made possible thanks to grant PIP 5262, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), to the authors. We thank Osvaldo Morrone for providing suggestions that greatly benefited an earlier version of the manuscript.

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illeg., non *Bertolonia* Spin, 1809. TYPE: *Pilopus nodiflora* Raf. [= *Phyla nodiflora* (L.) Greene].

Diototheca Raf., Fl. Ludov. 74. 1817. TYPE: *Diototheca repens* Raf. [= *Phyla nodiflora* (L.) Greene].

Cryptocalyx Benth., Ann. Nat. Hist., 2(12): 446. 1839. TYPE: *Cryptocalyx nepetifolia* Benth. [= *Phyla betulifolia* (Kunth) Greene].

Perennial, usually procumbent *herbs*, stems sometimes basally slightly woody, often rooting at nodes, usually densely covered with adpressed strigose, mostly malpighian (medifixed) acute hairs, rarely subglabrous. *Leaves* petiolate or subsessile; simple, decussate-opposite, margins entire or serrate-dentate. *Synflorescences* frondose, arranged in a homothetic pleiobotryum, the florescences solitary or to 3 per leaf axil, peduncled, spiciform or capitate and globose at anthesis, but later ovoid to oblong and cylindrical, densely flowered, with imbricate floral bracts. *Flowers* zygomorphic, perfect, sessile, small; floral bracts ovate to elliptic, apex often acute or acuminate, margin membranous; calyx persistent, membranous, compressed, keeled on each face, 2- to 4-dentate, subglabrous or pubescent with strigose, uncinate and glandular hairs; corolla hypocrateriform, tube straight or incurved, weakly exserted from calyx, mostly white, lavender to purple, limb 2-lipped, lobes broad or not; stamens 4, didynamous, included or sometimes slightly exserted, anthers not appendaged; ovary 1-carpellate, 2-locular, 1 ovule per locule, style terminal, stigma oblique. *Fruit* small, dry, obovoid to ellipsoid, included in the mature calyx and sometimes adnate to it, dividing at maturity into 2 nutlets, pericarp papyraceous.

Distribution. *Phyla* is widely distributed, growing in temperate, tropical and subtropical North and South America, with the exception of *P. nodiflora*, which is found on every continent.

Chromosome number. Lewis (1961) studied chromosome numbers for several *Phyla* species—*P. lanceolata* (Michx.) Greene, *P. nodiflora*, and *P. nodiflora* var. *reptans* (Kunth) Moldenke (sub. nom. *P. strigulosa* (M. Martens & Galeotti) Moldenke)—and consistently reported a diploid number of $2n = 36$, suggesting that this chromosome number seemed to be frequent in the genus. Additional chromosome counts reported for the widespread taxon known as *P. nodiflora* have also been $2n = 36$ (Covas & Schnack, 1946; Sharma, 1970; Bir & Sidhu, 1980).

Taxonomic Key to Species of *Phyla*

1a. Florescences 2 to 3 per axil; leaves with a petiole 1–2 cm long ..... 1. *P. betulifolia*

1b. Florescences 1 per axil; leaves sessile or subsessile 2

2a. Leaves thick and coriaceous, margins entire or with 1 to 3 pairs of teeth 3

2b. Leaves chartaceous, margins entire, serrate or teethed 4

3a. Leaf blade oblong to obovate, 1–5 × 0.5–1 cm, base cuneate ..... 2. *P. cuneifolia* (Torr.) Greene

3b. Leaf blade linear, 1.5–3 × 0.3–0.4 cm, base connate to the opposite leaf ..... 4. *P. linearis* (Kunth) Tronc. & López-Pal.

4a. Leaf blades elliptic; subglabrous with slightly adpressed strigose pubescence; plants restricted to the United States ..... 3. *P. lanceolata*

4b. Leaf blades obovate, spatulate, or ovate to rhombic-ovate; subglabrous with slightly adpressed strigose pubescence; if blades elliptic then with canescent pubescence and white strigose hairs; plants distributed worldwide ..... 5. *P. nodiflora*

1. Phyla betulifolia (Kunth) Greene, Pittonia 4: 48. 1899. Basionym: *Lippia betulifolia* Kunth, Nov. Gen. Sp. [H.B.K.] (quarto ed.) 2: 264. 1818. TYPE: Venezuela. Apure: San Fernando, s.d., *F. W. Humboldt & A. Bonpland 1139* (holotype, P-604475 not seen, P-604475 photo at SI!; isotypes, B-W 11121-01 not seen, B-W 11121-01 photo at SI!, P-307284 not seen, P-307284 photo at SI!, P-307283 not seen, P-307283 photo at SI!, photo F neg. 39487!). Figure 1.

Cryptocalyx nepetifolia Benth., Ann. Nat. Hist. 2(12): 446. 1839. TYPE: British Guiana. Berbice, s.d., *R. Schomburgk 694* (lectotype, selected here, K not seen, K photo at SI!; duplicates of lectotype, BM not seen, BM photo at SI!; TCD not seen, TCD photo at SI!).

Perennial *herbs*, 15–60 cm, base woody, flowering stems erect, branches decumbent, rooting at nodes, generally with strigose and malpighiaceous hairs. *Leaves* with petioles 1–2 cm; blade ovate to nearly rhombic-ovate, 2–7(–9) × 1.5–5 cm, chartaceous or submembranous, venation prominent abaxially, slightly impressed adaxially; strigose pubescence and malpighiaceous hairs on both surfaces; base cuneate and decurrent, margins serrate from the widest part of the blade to the apex, the teeth mucronate, apex acute. *Florescences* ovoid to oblong spikes, 2 to 3 per axil, 1 × 0.3–0.5 cm at anthesis, elongating to 1.2 cm at maturity; short peduncles generally 0.5–0.8 cm, not surpassing leaves, flowers forming vertical lines in the spike; *floral bracts* elliptic, 2–3 mm, abruptly contracted to acuminate apex 0.8–1.5 mm, strigose hairs along margins and malpighiaceous hairs on abaxial surface, glabrous adaxially; *calyx* 0.8 mm, lobed to not more than half the length of the calyx, membranous with thickened lateral edges, margins with short scattered glandular hairs and short strigose hairs; *corolla* generally white,

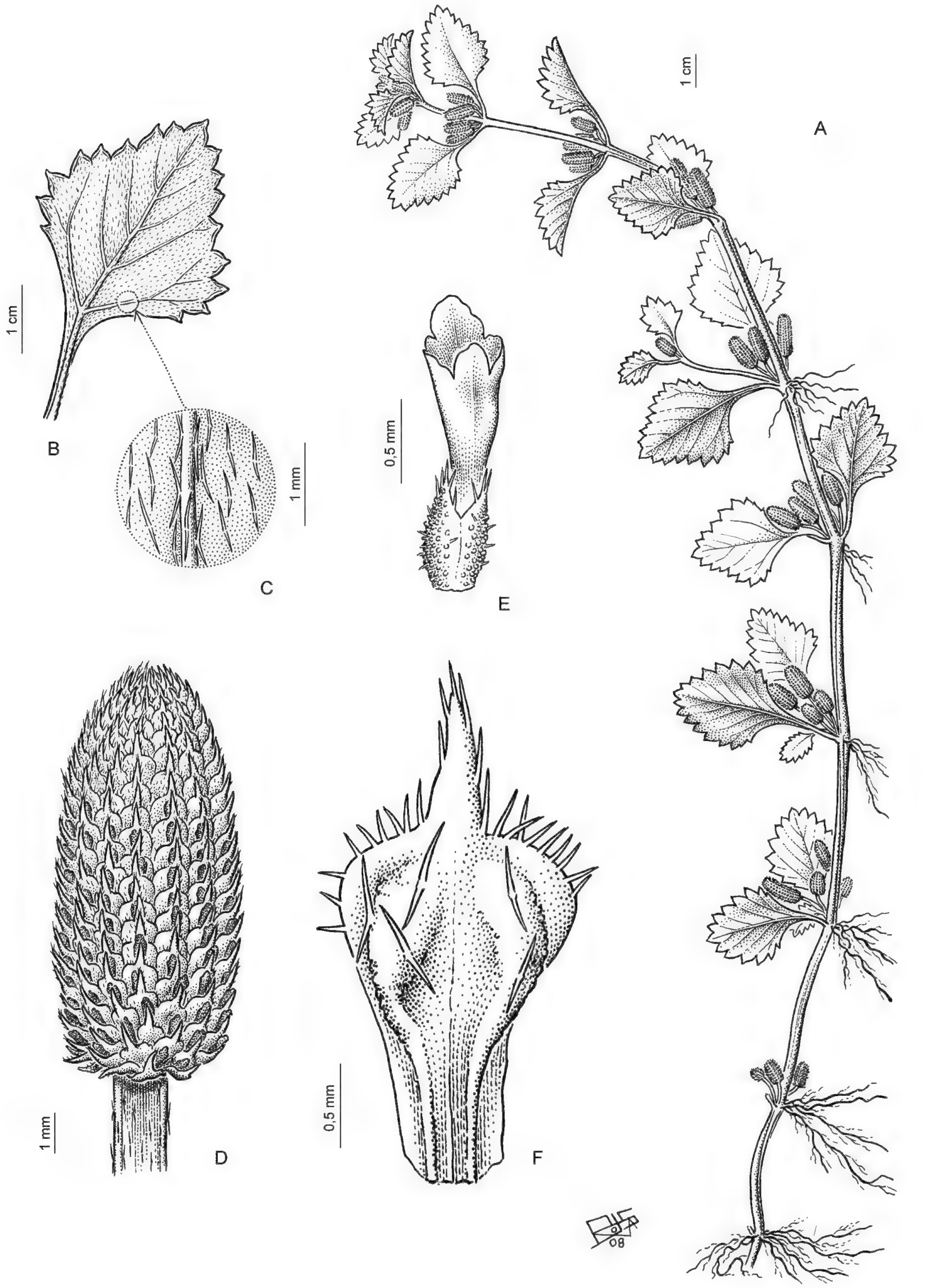


Figure 1. *Phyla betulifolia* (Kunth) Greene. —A. General aspect of plant. —B. Abaxial leaf surface. —C. Detail of pubescence of abaxial leaf surface. —D. Detail of florescence. —E. Flower. —F. Floral bract. A–C from *Rojas 2523* (SI); D, F from *Rojas 1884* (SI).

pale pink or pale purple, 1.8–2 mm, glabrous inside and outside except a narrow band of short hairs at the base of the lobes, lobes brief, erect, not conspicuous. *Fruit* dry, brown to yellow, each cluse 1 mm, obovoid, apex elongate.

Distribution and habitat. Collections of *Phyla betulifolia* have been made from Costa Rica, Guatemala, Honduras, and Panama in Central America, from Cuba and Trinidad in the West Indies, and from Bolivia, Brazil, Colombia, Ecuador, Paraguay, and Venezuela in tropical South America. It grows in low grounds, riverbanks and open woods, savannas, pastures and ruderal places, and is often found in sandy or clay soil.

Phenology. In Central America, *Phyla betulifolia* flowers principally between February and July and in South America mostly between July and November, so it can be found flowering in all seasons across this range.

Taxonomic notes. This species is easily recognized by its leaves that are ovoid to almost rhombic, with distinct petioles, and also by the presence of two or three shortly peduncled florescences at each leaf axil, floral bracts with conspicuous apices (cf. Fig. 1F), and minute flowers. All other species of *Phyla* have solitairy florescences in leaf axils and leaves that are sessile or subsessile and never petiolate.

In his protologue for *Cryptocalyx nepetifolia*, Bentham cited two collections: *Gardner 1049* (G not seen, G photo SI!, S not seen, S photo SI!, US not seen, US photo SI!) and *Schomburgk 694* (BM not seen, BM photo SI!, K not seen, K photo SI!). Thus, a lectotype is designated, with *Schomburgk 694* at Kew chosen because it is a complete and well-preserved specimen. Bentham (1839) states that *Cryptocalyx* differs from *Lippia* by its tenuous calyx, its small corolla limb, the complete separation of the fruit, and its capituliform florescences. Our analyses of the type material support that Bentham's concept of *Cryptocalyx* refers to *Phyla*.

Selected specimens examined. CUBA. **Oriente [Granma]:** Manzanillo, Sabana del Mar, *Ekman 5645* (US). **Pinar del Río:** San Cristóbal, *Ekman 13750* (US). COSTA RICA. **Alajuela:** San Carlos, Los Chiles, *Zamora 1404* (MO). EL SALVADOR. **Ahuachapán:** Santa Rita, *Rosales 2216* (MO). GUATEMALA. **Izabal:** Quirigua, *Standley 23865* (US). HONDURAS. **Atlántida:** La Fragua, *Standley 55685* (US). NICARAGUA. **Río San Juan:** San Carlos, *Seymour 5351* (MO). **Zelaya:** Bonanza through Constancia, *Stevens 8026* (MO). PANAMA. **Panamá:** La Jagua, *Bartlett 16371* (MO). TRINIDAD. St. Augustine lands, Imperial College of Tropical Agriculture, *Broadway 7206* (MO, US). BOLIVIA. **Pando:** Madre de Dios, *Beck 20455* (SI). BRAZIL. **Acre:** Tarauacá, *Prance 7347* (MO). **Amazonas:** Ilha das Oncas, *Mexia 6068* (MO, US). **Bahia:** Livramento do Brumado, lagoa da Jurema, *Harley 25868* (MO). **Pernambuco:** Recife, *Vasconcellos Sobinho 4099* (US); s. loc., *Gardner 1049* (syntype of *Cryptocalyx nepetifolia*, G, S, US). **Rondônia:** Porto Velho, *Duarte 7317* (SI). COLOMBIA. **Amazonas:** Río Loretoyacu, *Evans Schultes 6597* (US). **Antioquía:** Puerto Berrio, *Archer 1402* (US). **Bolívar:** San Martín de Loba, El Garcero, *Ramirez Arango 4597* (MO). **Boyacá:** Los Llanos, *Haught 2825* (US). **Santander:** Boca Sogamoso, río Magdalena, *Pennell 3840* (US). ECUADOR. **Guayas:** Balao, *Eggers 14275* (US). GUYANA. **Demerara-Mahaica:** Jct. Sheriff St. & David St., *Hill 27103* (US). **Pomeroon-Supenaam:** Lama Guest House, *Dowell 4172* (US). **Upper Takutu-Upper Essequibo:** Rewa River, *Clarke 3861* (US). PARAGUAY. **Alto Paraguay:** Itapucumí, playas río Paraguay, *Rojas 2523* (SI); Paraguay septentrionalis, *Hassler 7553* (BM). **Concepción:** Itacurubí, río Paraguay, *T. Rojas 1884* (SI). PERU. **Loreto:** Iquitos, río Itaya, *R. Scolnik 1164* (SI). **Tumbes:** Rivera izquierda río Tumbes, *López & Sagástegui 4024* (SI). **Ucayali:** Coronel Portillo, Yarinacocha, *Graham 363* (MO). VENEZUELA. **Amazonas:** Río Negro, río Casiquiare, *Stergios 8135* (MO). **Apure:** Puerto Piez, *Velez 2242* (US). **Carabobo:** Valencia, *Saer 827* (US). **Cojedes:** betw. S. Carlos & S. Rafael, *Pittier 11722* (US). **Delta Amacuro:** Paloma, *Rusby 6* (US). **Guárico:** orillas río Manati, 4 Dec. 1923, *Mayuel Grisol s.n.* (SI). **Monagas:** Boca de Uracoa, *Tamayo 3525* (SI). **Portuguesa:** Río Guanare & río Tucupido, *Liesner 12409* (MO).

2. Phyla cuneifolia (Torr.) Greene, Pittonia 4: 47. 1899. Basionym: *Zapania cuneifolia* Torr., Ann. Lyceum Nat. Hist. New York 2: 234. 1828. *Lippia cuneifolia* (Torr.) Steud., Nom. Bot. [Steudel], ed. 2, 2: 54. 1841. TYPE: U.S.A. Nebraska: "on the Platte," June 1820, *James s.n.* (holotype, NY not seen, NY photo at SI!). Figure 2.

Perennial *herbs*, 10–20(–30) cm, base woody, flowering stems sometimes ascending, branches decumbent, rooting at the nodes, generally conspicuously canescent with white strigose and malpighiaceous hairs. *Leaves* sessile; clustering in axils; blade oblong to obovate, 1–5 × 0.5–1 cm, thick and coriaceous, midvein prominent abaxially, slightly impressed adaxially; canescent pubescence of strigose and malpighiaceous hairs on both surfaces; base cuneate, margins entire or with 2 to 3 pairs of acute shallow teeth, apex acute. *Florescences* ovoid to oblong spikes, 1 per axil, 1 × 1 cm at anthesis, elongating to 2 cm at maturity; peduncles briefly surpassing leaves, generally 1–5 cm; *floral bracts* ovate, 3–5 mm, acute apex, adpressed canescent pubescence with malpighiaceous hairs on abaxial surface, glabrous adaxially; *calyx* 2.5 mm, lobed to not more than half the length of the calyx, membranous with thickened lateral edges, margins densely uncinate; *corolla* purple or white, 3–5 mm, glabrous inside and outside except a narrow band of

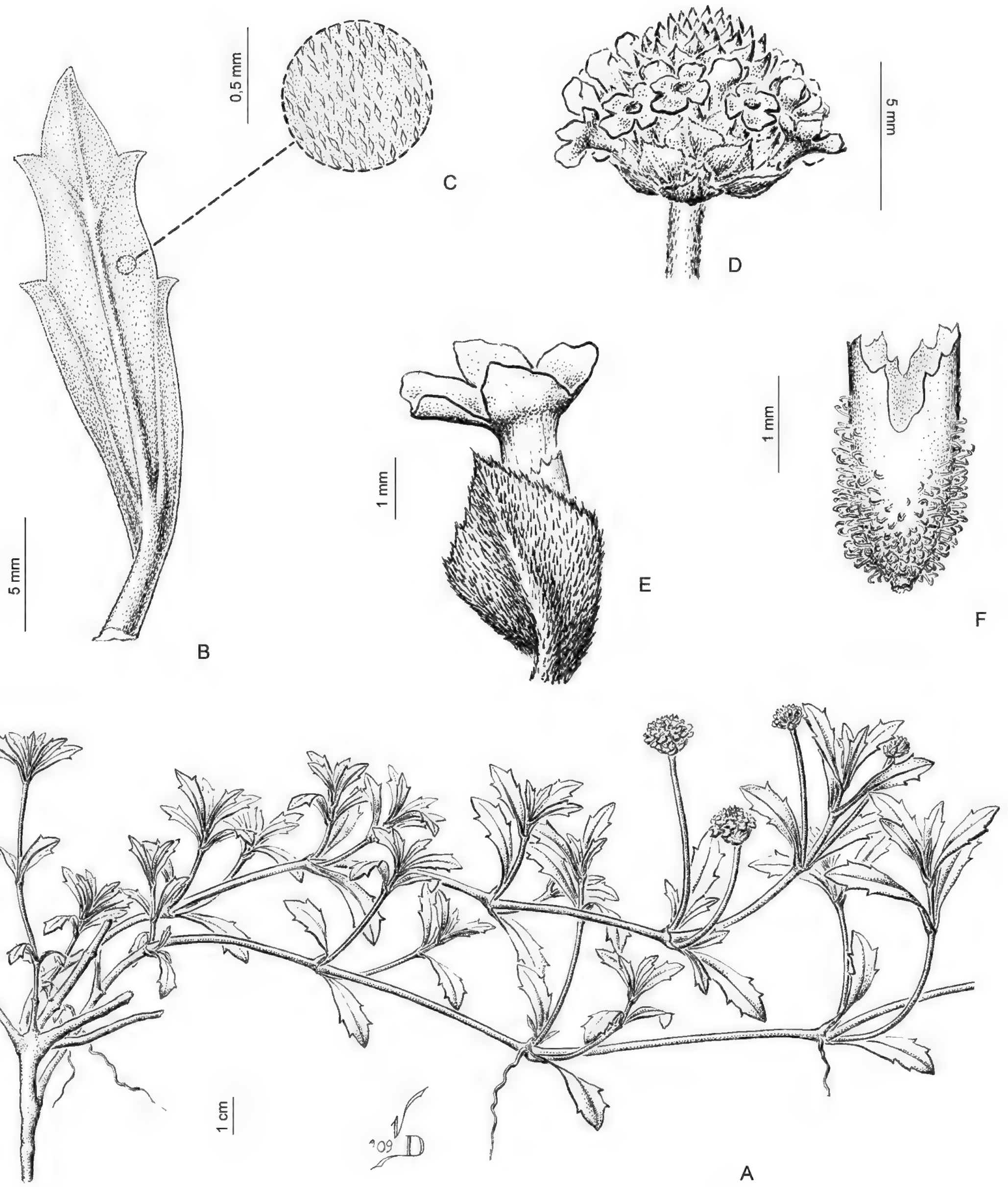


Figure 2. *Phyla cuneifolia* (Torr.) Greene. —A. General aspect of plant. —B. Abaxial leaf surface. —C. Detail of pubescence of abaxial leaf surface. —D. Detail of florescence. —E. Flower with floral bract. —F. Calyx. Drawn from *Crandall s.n.* (MO).

short hairs at the base of the developed lobes. *Fruit* dry, brown to yellow, each cluse 2 mm, elliptic.

Distribution and habitat. *Phyla cuneifolia* is endemic to the central and western United States, where it is found in dry areas, growing in disturbed sandy soils or riverbanks and marshes. Greene (1899: 47) mentioned that it is a strongly halophilous species, common on moist subsaline or alkaline plains.

Phenology. This species is found as flowering in May, June, and July.

Taxonomic notes. *Phyla cuneifolia* is readily distinguished by its thick and coriaceous leaves, versus chartaceous or submembranous leaves in *P. betulifolia*, *P. lanceolata*, and *P. nodiflora*. The only taxon that shares similar thick and coriaceous leaves is *P. linearis*, which is differentiated by its linear

blades with connate bases, whereas *P. cuneifolia* is distinguished by its oblong to obovate blades with cuneate base.

Selected specimens examined. U.S.A. **Arizona:** Navajo, S Holbrook, 31 July 1896, *Luck s.n.* (MO). **Colorado:** Larimer, Ft. Collins, 20 June 1896, *Crandall s.n.* (MO, US). **Kansas:** Kearny, 13 mi. SW Lakin, *Rydberg 922* (MO). **Nebraska:** Phelps, N Loomis, *Tolstead 411082* (MO). **New Mexico:** Socorro, San Antonio, *Ferris 2317* (MO). **Oklahoma:** Alfalfa Co., Ingersoll, *Stevens 624* (SI). **Texas:** Tascosa, *Reverchon 3254* (MO). **Wyoming:** Platte, Uva, *Nelson 387* (US).

3. Phyla lanceolata (Michx.) Greene, Pittonia 4: 47. 1899. Basionym: *Lippia lanceolata* Michx., Fl. Bor.-Amer. 2: 15. 1803. *Lippia nodiflora* (L.) Michx. var. *lanceolata* (Michx.) Alph. Wood, Class-book Bot., ed. 2, 413. 1847, non Kuntze, Revis. Gen. Pl. 2: 508. 1891, nom. illeg. TYPE: U.S.A. [South] Carolina: near Ashley River, 1787–1796, *Michaux s.n.* (holotype, P not seen, P photo at SI!; isotype, P not seen, P photo at SI!). Figure 3.

Lippia nodiflora var. *acutifolia* Kuntze, Revis. Gen. Pl. 2: 508. 1891. TYPE: U.S.A. Ohio: Hamilton Co., Cincinnati, 20 Aug. 1874, *O. Kuntze 2736* (holotype, NY not seen, NY photo at SI!).

Lippia lanceolata var. *recognita* Fernald & Griscom, Rhodora 37: 178. 1935. *Phyla lanceolata* var. *recognita* (Fernald & Griscom) Soper, Trans. Roy. Canad. Inst. 34: 35. 1962. TYPE: U.S.A. Iowa: Freemont Co., 30 July 1898, *T. J. Fitzpatrick s.n.* (holotype, GH not seen, GH photo at SI!).

Phyla lanceolata f. *ahlesii* Moldenke, Phytologia 4: 56. 1952. TYPE: U.S.A. Illinois: Iriquois Co., 4 mi. S Beaverville, 5 Aug. 1950, *H. Ahles 2560* (holotype, ILL not seen, ILL photo at SI!; isotype, F not seen).

Phyla nodiflora (L.) Greene var. *texensis* Moldenke, Phytologia 27: 69. 1973, syn. nov. TYPE: U.S.A. Texas. Bexar Co., betw. 1862 & 1889, *G. Jermy s.n.* (holotype, NY not seen, NY photo at SI!).

Perennial *herbs*, 25–50 cm, stems erect, branches sometimes procumbent, rooting at nodes; subglabrous or slightly adpressed, strigose pubescence with malpighiaceous hairs. *Leaves* subsessile; blade elliptic, 2–7.5 × 0.5–3 cm, chartaceous, midvein prominent abaxially, secondary venation less visible; subglabrous with slightly adpressed strigose pubescence and malpighiaceous hairs, base cuneate, margins serrate to the apex, with 5 to 8 pairs of acute teeth, apex acute, sometimes slightly subobtuse. *Florescences* ovoid to oblong spikes, 1 per axil, 1 × 0.7 cm at anthesis, elongating to 1.5–2.5 cm at maturity; peduncles 6–10 cm, surpassing leaves; *floral bracts* ovate, 2.5–3 mm, apex acute and contracted to acuminate or caudate, adpressed canescent pubescence with malpighiaceous hairs on abaxial surface, glabrous adaxially; *calyx* 2 mm, lobed to not more than half the length of the calyx, membranous with thickened lateral edges, margins glabrous with scattered adpressed hairs; *corolla* pale blue, purple, or white, 4 mm, glabrous inside and outside except for a narrow band of short hairs at the base of the developed lobes. *Fruit* dry, brown to yellow, each cluse 1.2–1.5 mm, obovoid.

Distribution and habitat. *Phyla lanceolata* is widely distributed in the central and eastern United States, where it is restricted and noted from moist soil, coastal marshes, and along riverbanks in soft sands and alluvial muds, but it is also found in much drier habitats.

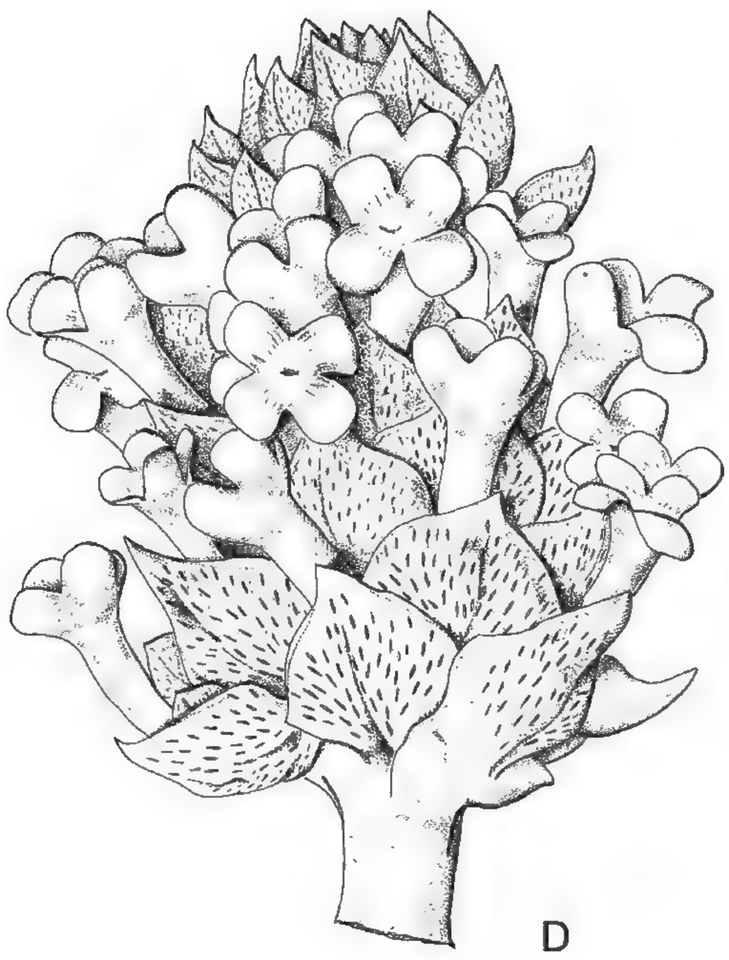
Phenology. This species flowers between May and September.

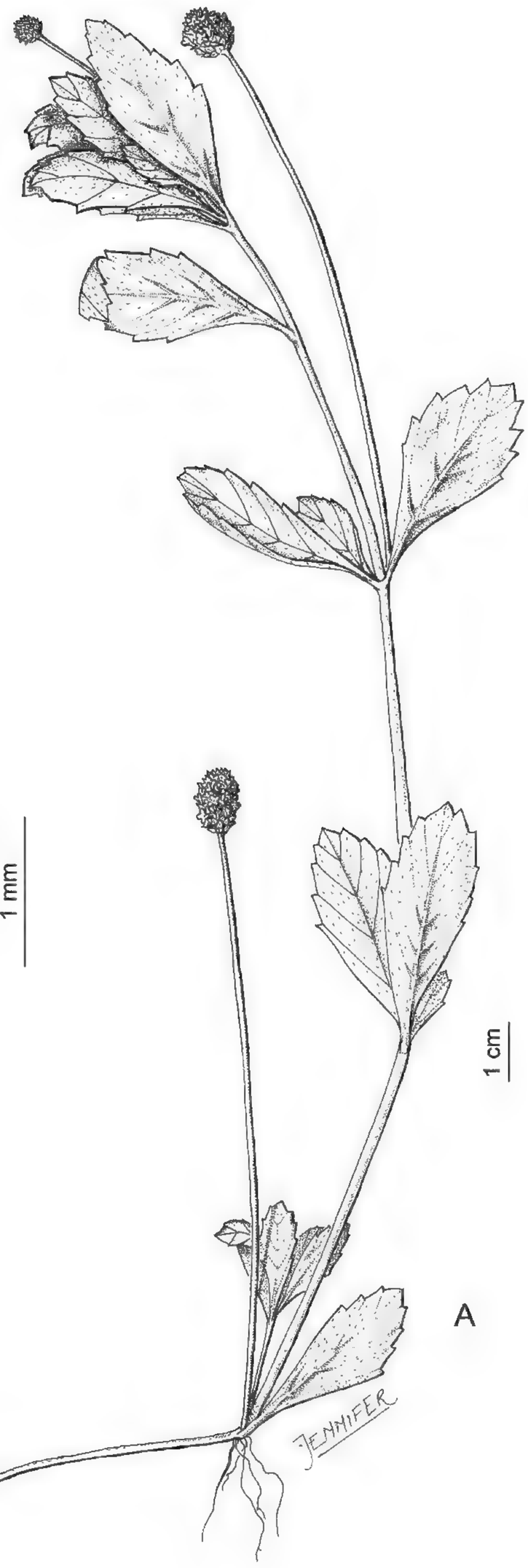
Taxonomic notes. *Phyla lanceolata* is distinguished by its perfectly elliptical leaves with regular margin serration, with five to eight pairs of acute teeth and its long peduncled florescences, 6–10 cm long. *Phyla nodiflora* var. *nodiflora* (L.) Greene is the most similar taxon morphologically, but its leaves are generally ovate to rhombic-ovate, spatulate or obovate. Sometimes blades are elliptic, as seen in *P. nodiflora* var. *minor* (Hook.) O'Leary & Múlgura; also, *P. nodiflora* var. *minor* has canescent pubescence with white strigose hairs (vs. subglabrous to slightly strigose leaf pubescence in *P. lanceolata*).

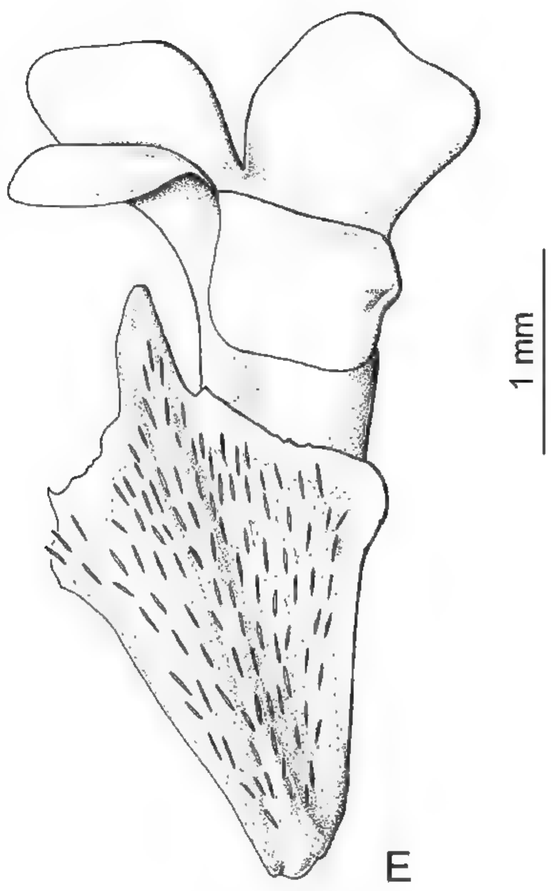
Moldenke (1973b) described *Phyla nodiflora* var. *texensis*, distinguishing it from the typical variety of *P. nodiflora* based on leaf morphology. However, our study of the type material indicates that this variety is the same taxon as *P. lanceolata*.

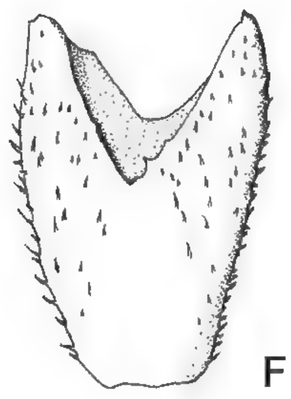
Sanders (2001: 347) observed that hybrids between this species and *Phyla nodiflora* exist in areas of sympatry between both taxa, as for example in coastal Virginia and Georgia, and in Lousiana, Oklahoma, and Texas.

Selected specimens examined. U.S.A. **Alabama:** limestone, *Isely 2824* (US). **Arkansas:** Baxter, *Hyatt 81* (MO). **California:** San Bernardino, *Roos 5306* (US). **District of Columbia:** Potomac River, *Herman 9631* (MO). **Florida:** Sarasota, *Tracy 7532* (US). **Georgia:** 1925, *Sperry 582* (US). **Illinois:** St. Clair, *Saunders 817B* (MO). **Indiana:** Bluffton, *Deam 1195* (US). **Iowa:** Fayette, *Fink 471* (US). **Kansas:** Riley, *Norton 394* (US). **Kentucky:** Robertson, *Braun 4056* (US). **Louisiana:** Iberia, *Thieret 21701* (US). **Maryland:** Dorchester, *Hotchkiss 7130* (US). **Michigan:** Wayne, 1916, *Chandler s.n.* (US). **Minnesota:** Carver Co., SSW Watertown, *G. A. Wheeler 20313* (SI). **Mississippi:** Oktibbeha, *Pollard 1310* (US). **Missouri:** St. Louis, *Taylor 5863* (MO). **Nebraska:** Saunders, Ashland, *Williams 349* (US). **New Jersey:** 1891, *Gross s.n.* (US). **New Mexico:** Chaves, *Earle 355* (US). **New York:** Cayuga, cross lake, *Muenscher 22049* (US). **North Carolina:** 1937, *Godfrey 4078* (US). **Ohio:** Greene, *Demaree 11445* (US). **Oklahoma:** Oklahoma Co., N Oklahoma City, *U. T. Waterfall 1336* (SI). **Pennsylvania:**









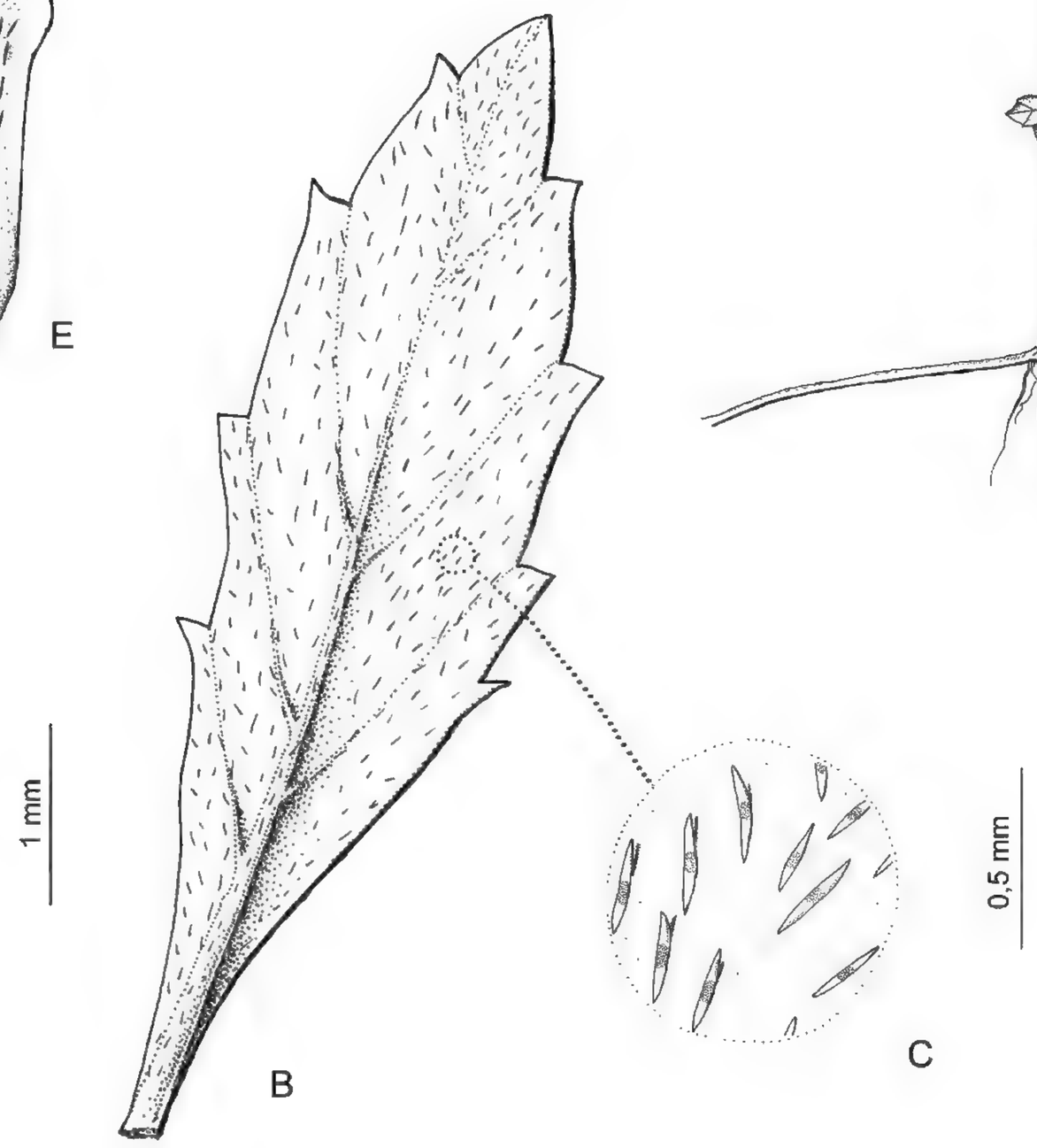


Figure 3. *Phyla lanceolata* (Michx.) Greene. —A. General aspect of plant. —B. Abaxial leaf surface. —C. Detail of pubescence of abaxial leaf surface. —D. Detail of florescence. —E. Flower with floral bract. —F. Calyx. Drawn from *Nee 43901* (SI).

Lancaster, 21 Sep. 1889, *Heller s.n.* (US). **South Carolina:** Beaufort, *Godfrey 1537* (US). **South Dakota:** 1940, *Johnson 98* (MO). **Tennessee:** Roane, *Nease 518* (US). **Texas:** Grayson Co., Sneed Environmental Research Area of Austin College, *Nee 43901* (SI). **Virginia:** Princess Anne, *Heller 1218* (US). **Washington:** 1896, *Steele s.n.* (MO). **Wisconsin:** La Crosse, *Swanson 2419* (MO).

4. Phyla linearis (Kunth) Tronc. & López-Pal., Pittieria 6: 19. 1974. Basionym: *Lippia linearis* Kunth, Nov. Gen. Sp. [H.B.K.] 2: 262, tab. 212. 1817. [1818]. TYPE: Venezuela. Sucre: Cumana, July 1800, *F. W. Humboldt & A. Bonpland 77* (holotype, P not seen, P photo SI from F neg. 39484!; isotype, P not seen, P photo at SI!).

Perennial *herbs*, 15 cm, base woody, stems erect, branches quadrangular; glabrate with malpighiaceous hairs. *Leaves* sessile, blade linear, 1.5–3 × 0.3–0.4 cm, thick and coriaceous, midvein prominent abaxially, subglabrous with slight adpressed strigose and malpighiaceous hairs, base connate to the opposite leaf, margins entire or occasionally with 1 to 3 teeth near apex, apex acute. *Florescences* ovoid spikes, 1 per axil, 0.5 × 0.5 cm at anthesis, elongating 1.5–2 cm at maturity; peduncles 1 cm, shorter than the leaves; *floral bracts* ovate, 2 mm, acute apex, adpressed canescent pubescence on abaxial surface; *calyx* 1–2 mm, lobed to not more than half the length of the calyx, membranous with thickened lateral edges, margins glabrous with scattered adpressed hairs; *corolla* white, 2–3 mm, glabrous inside and outside except for a narrow band of short hairs at the base of the developed lobes. *Fruit* dry, brown to yellow, each cluse 1 mm, obovoid.

Distribution and habitat. *Phyla linearis* is known only from the type specimen, collected by A. Bonpland, growing in sandy soils near Cumaná, Venezuela.

Phenology. This species was collected as flowering in July.

Taxonomic notes. Examination of the type specimen of *Phyla linearis* from type photographs, as well as the description in the protologue, indicates that this taxon differs from all other taxa in *Phyla*. This species is uniquely distinguished by its linear leaf blades with the blade base connate to the opposite leaf at the stem node. It shares with *P. cuneifolia* the thick and coriaceous leaf texture, with entire margins, but occasionally with one to three teeth near the apex. It is distinguished from *P. cuneifolia* by its cuneate leaf base and oblong to obovate leaf blade.

This species was not illustrated because no material could be found; however, there is a lamina in the *Flora de Venezuela* (López-Palacios, 1977: 487, fig. 114).

5. Phyla nodiflora (L.) Greene, Pittonia 4: 46. 1899. Basionym: *Verbena nodiflora* L., Sp. Pl. 1: 20. 1753. *Blairia nodiflora* (L.) Gaertn., Fruct. Sem. Pl. 1: 266, t. 56. 1788. *Zapania nodiflora* (L.) Lam., Tabl. Encycl. 1: 59, t. 17. 1791. *Lippia nodiflora* (L.) Michx., Fl. Bor.-Amer. (Michaux). 2: 15. 1803. *Platonia nudiflora* Raf., Med. Repos. 5: 352. 1808, nom. illeg. *Lippia nodiflora* var. *normalis* Kuntze, Revis. Gen. Pl. 2: 508. 1891. TYPE: Herb. Clifford: 11, *Verbena 3* (lectotype, designated by Townsend [1982: 32], BM-000557561 not seen, BM-000557561 photo at SI!).

Perennial *herbs*, 3–60 cm, stems procumbent or erect, flowering branches sometimes erect, rooting at nodes; subglabrous to adpressed strigose or canescent pubescence with malpighiaceous hairs. *Leaves* subsessile; blade elliptic, obovate, spatulate, or ovate to rhombic-ovate, 0.7–8 × 0.2–3 cm, chartaceous, only midvein prominent abaxially or pinnate venation prominent abaxially; subglabrous with slightly adpressed strigose pubescence or canescent pubescence with white strigose hairs and malpighiaceous hairs; base decurrent into the petiole, or cuneate, margins entire, serrate or with teeth toward the distal part of the blade, or all along the margin; apex subobtuse or acute. *Florescences* ovoid to oblong spikes, 1 per axil, 1 × 0.5–1 cm at anthesis, elongating to 1.5–6(–7) cm at maturity; peduncles long, surpassing leaves, 3–10 cm; *floral bracts* ovate to elliptic, 2–4 mm, acute-acuminate apex, adpressed canescent pubescence on abaxial surface with malpighiaceous hairs, glabrous adaxially; *calyx* 1.5–2.5 mm, lobed to not more than half the length of the calyx, membranous with thickened lateral edges, margins with scattered adpressed and uncinate hairs; *corolla* white, mauve, pink, pale blue, purple, or lilac, 3–4.5 mm long, glabrous inside and outside except for a narrow band of short hairs at the base of the developed lobes. *Fruit* dry, brown to yellow, each cluse 1.2–2 mm, obovoid to spherical.

Distribution and habitat. *Phyla nodiflora* is the most widely distributed taxon in *Phyla*, being found worldwide in tropical to temperate regions.

Taxonomic notes. There are three varieties of *Phyla nodiflora* principally distinguished by leaf morphology, margins, and venation. Moldenke (1939: 295) previously considered this taxon to be integrated by three varieties. These varieties are recognized here, although not under the same names.

Verdcourt (1992: 26) designated *Clayton 448* (BM) as the lectotype of *Verbena nodiflora*. The specimen had been seen by Linnaeus, so it may well be original material for the name. However, the earlier effective lectotypification was published previously by Townsend (1982).

TAXONOMIC KEY TO THE VARIETIES OF *PHYLA NODIFLORA*

1a. Leaf blades ovate to rhombic-ovate; pinnate venation prominent abaxially; margins serrate all along blade margin with 8 to 10 pairs of teeth or toothed toward the distal part of the blade .. .. 5c. *P. nodiflora* var. *reptans*

1b. Leaf blades obovate, spatulate or elliptic; only midvein prominent abaxially; margins entire or serrate toward the distal part of the blade, with 3 to 8 pairs of teeth 2

2a. Leaf blades elliptic or obovate, 0.5–2(–4) × 0.2–1 cm, apex mostly acute, canescent or white strigose pubescence .... 5b. *P. nodiflora* var. *minor*

2b. Leaf blades obovate, spatulate, 2–4(–7.5) × 0.5–1.5(–3) cm, apex mostly subobtuse, subglabrous or slightly adpressed strigose pubescence .... 5a. *P. nodiflora* var. *nodiflora*

5a. Phyla nodiflora (L.) Greene var. **nodiflora.** Figure 4A–H.

Verbena capitata Forssk., Fl. Aegypt.-Arab. 10. 1775. TYPE: [Egypt.] "Rosetta ad littora Nili. Succus expreffus, multum in ufu in *Stranguria*," s.d., *P. Forsskal s.n.* (holotype, LD not seen, LD photo at SI!).

Phyla chinensis Lour., Fl. Cochinch. 66. 1790. *Piarimula chinensis* Raf., Fl. Tellur. 2: 102. 1836 [1837]. TYPE: China. Habitat inculta prope Cantone Sinarum, s.d., *J. Loureiro 661* (holotype, P not seen, P photo at SI!).

Verbena repens Bertol., Rar. Ital. Pl. Dec. 2: 27. 1806. *Zapania repens* (Bertol.) Bertol., Rar. Ital. Pl. Dec. 3: 27. 1810. *Lippia repens* (Bertol.) Spreng., Syst. Veg. (ed. 16) [Sprengel]. 2: 752. 1825. *Lippia nodiflora* (L.) Michx. var. *repens* (Bertol.) Schauer, Prodr. (DC.) 11: 586. 1847. TYPE: [Italy.] "Sarzanae in palustribus pratorium arenosorum di Marinella. Floret Augusto Septembri," 1805, *s. coll.* (holotype, BOLO not seen, BOLO photo at SI!).

Verbena sarmentosa Willd., Enum. Hort. Berol. Alt. 632. 1809. *Lippia sarmentosa* (Willd.) Spreng., Syst. Veg. 2: 752. 1825. *Lippia nodiflora* var. *sarmentosa* (Willd.) Schauer, Prodr. 11: 585. 1847. TYPE: [India.] "Habitat in India orientali," *Willdenow herbarium 11122* (holotype, B-W [fl.] not seen, B-W photo at SI!; isotypes, B-W [3] not seen, B-W [3] photos at SI!).

Lippia nodiflora var. *subsessilis* Bornm., Verh. Zool.-Bot. Ges. Wien 48: 615. 1898. *Phyla nodiflora* var. *subsessilis* (Bornm.) Moldenke, Phytologia 6: 447. 1959. TYPE: [Syrian Arab Republic] Palestina. Jaffa: Fruchtgarten, May 1897, *J. F. N. Bornmüller 1239b* (holotype, B not seen, B photo at SI!).

Phyla incisa Small, Fl. S.E. U.S. [Small]. 1012. 1903. *Lippia cuneifolia* (Torr.) Steud. var. *incisa* (Small) Blank., Rep. (Annual) Missouri Bot. Gard. 18: 186. 1907. *Lippia incisa* (Small) E. D. Schulz, Texas Wild Fls. 339. 1928. *Phyla nodiflora* var. *incisa* (Small) Moldenke, Phytologia 27: 69. 1973. TYPE: U.S.A. Texas: Nueces Co., Corpus Christi, 28–31 May 1894, *A. A. Heller 1806* (holotype, NY not seen, NY photo at SI!; isotypes, MICH not seen, MICH photo at SI!, MO not seen, MO photo at SI!, NY [2] not seen, NY [2] photos at SI!, UC not seen; UC photo at SI!, US not seen, US photo at SI!).

Lippia nodiflora var. *suborbicularis* Chevall., Bull. Herb. Boissier ser. 2, 5: 443. 1905. TYPE: Algeria. Biskra, Sep. 1903, *L. Chevallier 604* (holotype, P not seen, P photo at SI!; isotypes, NY not seen, NY photo at SI!, US not seen, US photo at SI!).

Phyla nodiflora var. *longifolia* Moldenke, Phytologia 2: 22. 1941. TYPE: Honduras. Atlántida: La Ceiba, beach at Salado, 10 July 1938, *T. G. Yuncker, J. M. Koepper & K. A. Wagner 8327* (holotype, NY not seen, NY photo at SI!; isotypes, MICH not seen, MICH photo at SI!, UC not seen, UC photo at SI!, US not seen, US photo SI!).

Phyla nodiflora f. *spathulata* Moldenke, Phytologia 4: 180. 1953. TYPE: Java. Batavia, 1902, *C. A. Backer s.n.* (holotype, BO-21889 not seen).

Phyla nodiflora var. *antillana* Moldenke, Phytologia 40: 468. 1978, syn. nov. TYPE: Virgin Islands of the United States: St. Croix, Judith's Fancy, 17–25 Mar. 1923, *E. G. Britton, N. L. Britton & J. F. Kemp 83* (holotype, NY not seen, NY photo at SI!).

Phyla nodiflora var. *galapagensis* Moldenke, Phytologia 41: 450. 1979. TYPE: Ecuador. Galápagos Islands: Santa Cruz Island, near the Caseta, Oct. 1974, *H. H. van der Werff 1592* (holotype, NY not seen, NY photo at SI!; isotype, CAS not seen, CAS photo at SI!).

Plants 20–60 cm, stems procumbent or sometimes erect; adpressed strigose pubescence with malpighiaceous hairs. *Leaf* blade obovate, spatulate, 2–4(–7.5) × 0.5–1.5(–3) cm, only midvein prominent abaxially; subglabrous or with slightly adpressed strigose pubescence and malpighiaceous hairs; margins entire or serrate toward the distal part of the blade, with 4 to 8 pairs of acute teeth; apex subobtuse, sometimes acute. *Florescences* oblong spikes, 1 × 0.7–1 cm at anthesis, elongating to 1.5–3 cm at maturity; *corolla* white, fading to pink, 4–4.5 mm long.

Distribution and habitat. *Phyla nodiflora* var. *nodiflora* is widely distributed, found principally in the Americas, from the United States to the south, extending into Argentina and Chile. The majority of the individuals examined were from Central America (Belize, Honduras, Nicaragua, Panama, and Puerto Rico) and the Antilles (Bahamas, Barbados, Bermuda, Cayman Islands, Cuba, Dominican Republic, Guadaloupe, Haiti, and Martinique). This species is also noted from Africa (Algeria, Angola, Botswana, Egypt, Eritrea, Ethiopia, Madagascar, Malawi, Morocco, Mozambique, Senegal, Seychelles, South Africa, Swaziland, Tanzania, Togo, Tunis, Uganda, and Zaire), Asia (China, the Philippines, India, Indonesia, Iran, Japan, Saudi Arabia, and Sri Lanka), Oceania (Australia, Caroline Islands, Guam, Hawaii, New Caledonia, New Guinea, Northern Mariana, and

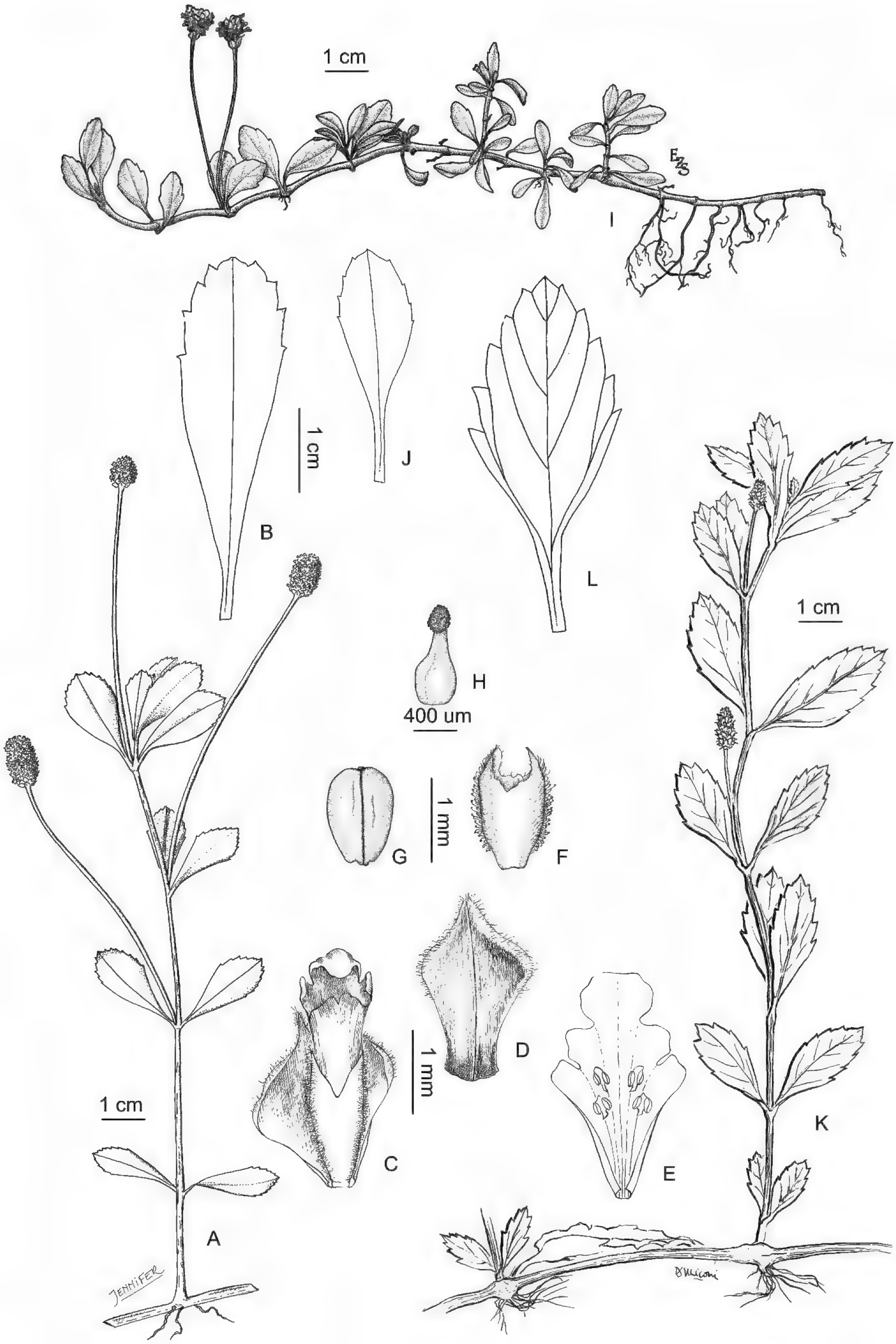


Figure 4. A–H. *Phyla nodiflora* (L.) Greene var. *nodiflora*. —A. General aspect of plant. —B. Adaxial leaf surface. —C. Flower with floral bract. —D. Floral bract. —E. Extended corolla. —F. Calyx. —G. Fruit. —H. Gynoecium. I, J. *P. nodiflora* var. *minor*. —I. General aspect of plant. —J. Adaxial leaf surface. K, L. *P. nodiflora* var. *reptans*. —K. General aspect of plant. —L. Adaxial leaf surface. Scale for J and L is the same as scale for B. A, B from *Bradley 1215* (MO); C–I, K redrawn from Troncoso and Botta (1993: 78, fig. 35); J from *Boelcke 6676* (SI); L from *Steinbach 2888* (SI).

Solomon Islands), and Europe (France and Spain). *Phyla nodiflora* var. *nodiflora* is found in disturbed soils, roadsides, and ponds, and on the borders of marshes or lakes, wherever soil has a regular water source.

Phenology. *Phyla nodiflora* var. *nodiflora* flowers in all seasons.

Taxonomic notes. There is a certain phenotype, which we do not recognize at formal taxonomical rank, but do mention as described by Small as *Phyla incisa* (Small, 1903), later treated as *P. nodiflora* var. *incisa* (Moldenke, 1973a). This corresponds to what Moldenke previously noted as *P. nodiflora* var. *longifolia*, a name synonymized herein (Moldenke, 1941). This phenotype is characterized by plants with narrow, thick-textured leaves, serrate at the apex, and has been identified in collections from Texas (*Runyon 440*, US) and Arkansas, U.S.A. (*Demaree 17288*, MO), Chihuahua, Mexico (*Waterfall 12497*, US), and Atlántida, Honduras (*Standley 53825*, US). This phenotypic variability could be related to soil condition and high temperature, because these plants were noted to grow in sandy, dry areas. We should mention one additional geographical phenotype from Sri Lanka, which has small leaves to 2 cm long and blade margins regularly crenate toward the apex (*Sumithraarachchi 779A*, MO; *Bernardi 15673*, MO).

Although the protologue of *Verbena capitata* (Forsskal, 1775: 10) did suggest that this species was not the same as *V. nodiflora* L., our study of the type specimen confirms both taxa are the same.

Moldenke (1978: 468) described *Phyla nodiflora* var. *antillana*, distinguishing it from the typical variety by the margins of its leaf blades conspicuously spreading dentate, with large, narrow, triangular teeth, sharply acute apically. However, our study of the type material indicated that this variety should not be retained because no further difference was seen between the typical variety and this phenotype.

Selected specimens examined. MEXICO. **Campeche:** Carmen, *Mell 2011* (US). **Chihuahua:** Aug. 1956, *Waterfall 12497* (US). **Coahuila:** Saltillo, *Arsène 6334* (US). **Guerrero:** Coyuca, Ancón, *Hinton 5810* (US). **Jalisco:** Paso de la Troje, *McVaugh 16908* (US). **México:** Zumpango, San Juan Citlaltepec, *Jacquemin 1221* (SI). **Michoacán:** Río Balsas, *Langlassé 145* (US). **Nuevo León:** Monterrey, *Pennell 16782* (US). **Oaxaca:** Juchitán, *King 352* (US). **Puebla:** Cholula, 26 Aug. 1907, *Arsène s.n.* (US). **Quintana Roo:** Coba, *Lundell 7792* (US). **Sinaloa:** San Blas, *Maltby 14* (US). **Sonora:** Fronteras, *Hartman 16* (US). **Veracruz:** Laguna, *Greenman 32* (US). **Yucatán:** Merida, *Souza Novelo 260* (US). U.S.A. **Arkansas:** Pulaski, *Demaree 17288* (MO). **California:** Sacramento, 1895, *Ward s.n.* (SI). **Florida:** Lee, Fort Myers, *Deam 60610* (SI); Santa Rosa Co., Hwy. 87, *Bradley 1215* (MO). **Georgia:** Lanier, *Clewel 2595* (MO). **Louisiana:** Alexandria, *Ball 419* (MO). **Missouri:** 1895, *Bush 471* (MO). **North Carolina:** 1885, *McCarthy s.n.* (US). **Oklahoma:** Payne, *Stratton 213* (MO). **South Carolina:** Beaufort, *Dorr 941* (MO). **Texas:** Brownsville, *Runyon 440* (US). BAHAMAS. **Andros:** Coakley town, *Dawson 26764* (US). **Eleuthera:** Savannah sound area, *Webster 10745* (US). **Hog Island [Paradise Island]:** New Providence, *Wilson 8296* (US). **Long Island:** Clarence, *Hackett 156* (US). BARBADOS. **St. John:** Glenburnie, *Carrington 1867* (US). BELIZE. San Pedro de Sula, Ambergris Caye, 1980, *Dwyer 15056* (MO). BERMUDA. **Agar's Island:** 22 July 1913, *Collins 264* (US). CAYMAN ISLANDS. George Town, Sep. 1958, *Sachet 423* (US). CUBA. **Havana:** Isla de Pinos, *Morton 10293* (US). **Pinar del Río:** Palme Barrens, *Shafer 10623* (US). DOMINICAN REPUBLIC. **Barahona:** July 1910, *Fuertes 439* (US). **Duarte:** Macoris, Boca Chica, *Allard 14765* (US). **El Seibo:** Higüey, *Howard 9782* (US). **Independencia:** 1980, *Mejía 7137* (MO). **Puerto Plata:** Sep. 1954, *Jimenez 2737* (US). **Santo Domingo:** Puerto Plata, *Ekman 14516* (US). **Saona Island:** 8 July 1956, *Marcano 3372* (US). GUADALOUPE. **Îlet Boissard:** Mar. 1938, *Questel 663* (US). **Port-Louis:** 2 Mar. 1934, *Rodriguez 2912* (SI). **Sainte-Anne:** 19 Mar. 1936, *Rodriguez 4179* (SI). HAITI. Rochelois, 23 Mar. 1927, *Ekman 7904* (US). **Port-de-Paix:** 21 Dec. 1928, *Leonard 11023* (US). **Port-au-Prince:** Apr. 1920, *Leonard 3436* (US). **Tortuga Island:** Mar. 1929, *Leonard 14093* (US). HONDURAS. **Atlántida:** Tela, *Standley 53825* (US). MARTINIQUE. **Sainte-Anne:** Jan. 1867/70, *Hahn 1338* (SI). NICARAGUA. **Granada:** June 1869, *Lévy 18* (SI). PANAMA. Canal Zone, Toro Point, 6 Oct. 1961, *Duke 4328* (MO). **Los Santos:** 1962, *Dwyer 2500* (MO). PUERTO RICO. Punto Cangrejos, Mar. 1914, *Stevenson 1690* (US). **[Guánica:]** Guánica Lake, Mar. 1935, *Sargent 11* (US). **Hamacao:** Aug. 1979, *García del Llano s.n.* (US). ARGENTINA. **Buenos Aires:** San Pedro, Isla Alonso, *Nicora 3472* (SI). **Chaco:** Gral. Güemes, Fortín Lavalle, *Pedersen 14001* (SI). **Córdoba:** Río Segundo, RN 9, *Subils 986* (SI). **Corrientes:** Esquina, *Krapovickas 26798* (SI). **Entre Ríos:** PN Predelta, June 2006, *Sosa s.n.* (SI). **Formosa:** Bermejo, La Rinconada, *Arenas 3091* (SI). **Jujuy:** Santa Bárbara, Lag. San Miguel, *Zuloaga 2834* (SI). **La Pampa:** Chalileo, río Salado en Santa Isabel, *Troiani 3611* (SI). **Mendoza:** 10 abr. 1937, *Burkart 8434* (SI). **Salta:** San Martín, Ruta 34, *Zuloaga 2655* (SI). **San Juan:** 25 de Mayo, Encón, *Haene 861* (SI). **San Luis:** s. loc., *Pastore s.n.* (SI). **Santa Fe:** Castellanos, ruta 34, Sunchales, *Burkart 30602* (SI). **Santiago del Estero:** Beltrán, *Maldonado 535* (SI). **Tucumán:** Leales, Chañar, *Venturi 486* (SI). BOLIVIA. **Tarija:** Avilez, cerca Chocloca, *Bastión 297* (SI). BRAZIL. **Rio Grande do Sul:** Torres, *Burkart 25147* (SI). CHILE. **Arica and Parinacota:** Tacna, *Shepard 277* (US). **Atacama:** 1985, *Zöllner 12790* (MO). **Tarapacá:** Mamiña, *Wiesenborn 13322* (SI). COLOMBIA. **Chocó:** Baudó, *Fuchs 22123* (US). **Cundinamarca:** Usaquén, 6 abr. 1908, *Apollinaire s.n.* (SI). **Magdalena:** Mar. 1948, *Romero 968* (US). **Nariño:** Tumaco, El Morro, *Idrobo 1431* (US). ECUADOR. **Galápagos Islands:** Santa Cruz, *Bentley 274* (MO). PARAGUAY. **Boquerón:** Ochoa, *Mereles 5514* (MO). **Presidente Hayes:** puente Remanso, *Mereles 1612* (SI). PERU. **Ancash:** 1986, *Francia 145* (MO). **Arequipa:** Islay, *FLSP 2453* (MO). **Cajamarca:** 1997, *Lewis 17365* (MO). **Callao:** Sep. 1923, *Macbride 5880* (US). **La Libertad:** Chicama valley, *Graywood Smyth 66* (US). **Lambayeque:** Chiclayo, Pimentel, *Fosberg 27986* (US). **Lima:** Chancay, *Cerrate 1624* (MO). **Tacna:** 1986,

Dillon 4753 (MO). URUGUAY. **Rocha:** Santa Teresa, *Cabrera 13610* (US). VENEZUELA. **Aragua:** represa Taiguaiguai, *Fernandez 629* (SI). **Carabobo:** Urama, *Burkart 16333* (SI). **Miranda:** Tacarigua, *Gines 4517* (US). **Zulia:** Mocquerys, 1893, *Drake s.n.* (SI). ALGERIA. **Hamma:** s. loc., 1876, *Reboud 1325* (MO). ANGOLA. Shella, s. loc., 1930, *s. coll.* (US). BOTSWANA. **North-East District:** s. loc., 1973, *Smith 704* (MO). EGYPT. **Abu Matamir:** s. loc., 1967, *Täckholm s.n.* (MO). ERITREA. Dangollo presso Ghinda, s. loc., 1902, *Pappi 4529* (US). ETHIOPIA. Gamo Gofa, s. loc., 1985, *Aweke 2445* (MO). **[Harari:]** Harar, Lake Alemaya, *Bunger 409* (US). MADAGASCAR. **Mahajanga:** s. loc., 2005, *Andriamihajarivo 821* (MO). Toamasina, s. loc., 7 Dec. 1984, *Dorr 3309* (US). MALAWI. **Chikwawa:** s. loc., 6 Oct. 1946, *Brass 17998* (US). **Dowa:** s. loc., 1992, *Goyder 3516* (MO). MOROCCO. Moulay-Bou-Selham, s. loc., 1973, *Davis 55600* (MO). MOZAMBIQUE. **Maputo:** s. loc., 1909, *Howard 5* (US). Lourenço Marques, s. loc., 29 Mar. 1948, *Rodin 4156* (US). SENEGAL. **Dakar:** s. loc., *Baldwin 5738* (US). SEYCHELLES ISLANDS. **Farquhar Atoll:** North Island, *Poore 1365* (US). **Praslin Island:** s. loc., 1992, *Kramer 11087* (MO). SOUTH AFRICA. Pretoria, s. loc., 1976, *Leistner 275* (MO). SWAZILAND. Mlawula Station, 3 Nov. 1977, *Kemp 1094* (US). TANGANYIKA [TANZANIA]. Ujiji, Mar. 1939, *Loveridge 711* (US). TOGO. trockener, 1973, *Hiepko 31* (MO). TUNISIA. **Gafsa:** 1908, *Pitard 467* (US). UGANDA. **Bunyoro:** Bujenje, 1977, *Katende 2841* (MO). ZAIRE [DEMOCRATIC REPUBLIC OF THE CONGO]. **Orientale:** Mahagi-Port, 1957, *Froment 244* (MO). CHINA. **Guangdong:** 2002, *S. Y. Hu 23885* (MO). PHILIPPINES. **Manila:** 1983, *Deguchi 6344* (MO). INDIA. **Rajasthan:** Dungerpur, *Verma 195* (MO). INDONESIA. **Tanimbar Islands:** Jamdena, *Pleyte 1* (US). IRAN. **Khuzestan:** 1964, *Grant 15894* (MO). JAPAN. **Kyushu:** Kagoshima, Odomari, *Ohba 201* (SI). SAUDI ARABIA. Khoba, 1976, *Dwyer 13638* (MO). SRI LANKA. **Batticaloa:** 1975, *Bernardi 15673* (MO). **Northern Province:** Mantai, 1975, *Sumithraarachchi 779A* (MO). FRANCE. **Corsica:** Barcaggio, *Julien 7* (SI). SPAIN. **Almería:** La Cañada, *Sennen 8158* (SI). AUSTRALIA. **Cobourg Peninsula:** 1994, *Egan 3143* (MO). CAROLINE ISLANDS. **Ulithi Atoll:** Asor islet, *Fosberg 46388* (US). GUAM. **Apra Harbor:** 14 May 1983, *Herbst 7152* (US). **Agana:** 13 July 1965, *Fosberg 46295* (US). HAWAII. **Oahu:** 1980, *Degener 35075* (MO). NEW CALEDONIA. **South Province:** Nouméa, Anse Vata, 8 Aug. 1950, *Bodenheim 5235* (US). NEW GUINEA. **Papua:** Woodlark Island, *Brass 28665* (US). NORTHERN MARIANA ISLANDS. **Rota:** Sinapalo, 26 Apr. 1982, *Herbst 6768* (US). **Saipan:** Puerto Rico, *Herbst 6879* (US). PALAU. **Peleliu:** *Emmons 90* (US). SOLOMON ISLANDS. **Ontong Java Atoll:** Luangiua, *Bayliss-Smith 16* (US). **Russell Islands:** Pavuvu, *Burcham 176* (US).

5b. Phyla nodiflora var. **minor** (Hook.) N. O'Leary & Múlgura, comb. nov. Basionym: *Lippia nodiflora* var. *minor* Gillies & Hook., Bot. Misc. 1: 171. 1830. TYPE: Argentina. Córdoba: "ad ripas fluminis Saladillo," s.d., *J. Gillies s.n.* (holotype, K not seen, K photo at SI!). Figure 4I, J.

Lippia canescens Kunth, Nov. Gen. Sp. [H.B.K.] (quarto ed.) 2: 263. 1818. *Zappania canescens* Gilbert, Enum. Pl. Montevideo 44. 1873. *Lippia nodiflora* f. *canescens* (Kunth) Kuntze, Revis. Gen. Pl. 2: 508. 1891. *Phyla canescens* (Kunth) Greene, Pittonia 4: 48. 1899. *Phyla nodiflora* var. *canescens* (Kunth) Moldenke, Phytologia 1: 98. 1934. TYPE: Peru. Trujillo: 1802, *F. W. Humboldt & A. Bonpland s.n.* (holotype, P not seen, P photo at SI!; isotype, SI!).

Lippia filiformis Schrad., Index Sem. (Gottingen): 4. 1834. *Phyla filiformis* (Schrad.) Meikle, Fl. Cyprus 2: 1249. 1985. TYPE: Chile. "from Chile, cult. Göttingen Bot. Gard.," s.d., *s. coll.* (holotype, GOET not seen).

Zappania nodiflora var. *rosea* D. Don in Sweet, Brit. Fl. Gard. [Sweet], 2nd. ser., 3: tab. 225. 1835. *Phyla nodiflora* var. *rosea* (D. Don) Moldenke, Phytologia 2: 22. 1941. *Lippia nodiflora* var. *rosea* (D. Don) Munz, Aliso 4(1): 97. 1958. *Lippia nodiflora* var. *rosea* (D. Don) J. F. Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser. 13(5): 651. 1960, nom. illeg. TYPE: Illustration from Sweet, 1835, in Brit. Fl. Gard., 2nd. ser., 3: pt. 225 (lectotype, designated by Munir [1993: 122]).

Lippia caespitosa Rusby, Mem. Torrey Bot. Club 6: 106. 1896. *Phyla caespitosa* (Rusby) Moldenke, Revista Sudamer. Bot. 5: 2. 1937. TYPE: Bolivia. Cochabamba: below Cochabamba, 1891, *M. Bang 1009* (holotype, NY not seen, NY photo at SI!; isotypes, MICH not seen, MICH photo at SI!, MO not seen, MO photo at SI!, NY [2] not seen, NY [2] photo at SI!, US [2] not seen, US [2] photo at SI!).

Lippia nodiflora var. *pusilla* Briq., Ark. Bot. 2(10): 19. 1904. *Phyla nodiflora* var. *pusilla* (Briq.) Moldenke, Phytologia 1: 170. 1935. TYPE: Brazil. Rio Grande do Sul: Rio Grande, 22 Nov. 1892, *C. A. Lindman A283-1/2* (holotype, S not seen, S photo at SI!).

Lippia subterranea Rusby, Descr. S. Amer. Pl. 108. 1920. *Phyla subterranea* (Rusby) Moldenke, Revista Sudamer. Bot. 5: 2. 1937. TYPE: Peru. Mollendo, 5 Aug. 1901, *R. S. Williams 2933* (holotype, NY not seen, NY photo at SI!).

Phyla nodiflora f. *copiapina* Acevedo, Bol. Mus. Nac. Hist. Nat. Santiago de Chile 25: 47. 1951, syn. nov. TYPE: Chile. Copiapó, frente al Río Copiapó, Nov. 1936, *M. R. Espinosa Bustos 5* (holotype, SGO-68293 not seen, SGO-68293 photo at SI!; isotype, NY not seen, NY photo at SI!).

Plants 3–15 cm, stems procumbent, flowering branches sometimes erect; generally conspicuously canescent pubescence with white strigose and malpighiaceous hairs. *Leaf* blade elliptic or obovate, 0.5–2(–4) × 0.2–1 cm, only midvein prominent abaxially; canescent pubescence with white strigose and malpighiaceous hairs on abaxial and adaxial surfaces; margins entire or serrate toward the distal part of the blade, with 3 to 7 spreading and well-spaced shallow teeth; apex mostly acute. *Florescences* ovoid to oblong spikes, with 2 to 4 whorls of open flowers, 1 × 0.5–1 cm at anthesis, elongating to 2–3 cm at maturity; *corolla* mauve or white, fading to pink or lilac, 3–4.5 mm long.

Distribution and habitat. *Phyla nodiflora* var. *minor* is found principally in temperate South America (Argentina, Bolivia, southern Brazil, Chile, Ecuador, Paraguay, Peru, and Uruguay), in which it is presumably native (Xu et al., 2010). The existence

of specimens of this variety in other parts of the world, as for example in North and Central America (United States, Mexico, Haiti, and Dominican Republic), Australia, Europe (France and Spain, Xu et al., 2010), or Africa (Egypt; Ethiopia; Free State, South Africa), is most certainly due to unintentional introduction of this taxon and its subsequent establishment by rapid adaptative evolution (Xu et al., 2010). This variety has been noted as an invasive perennial forb widespread in Australia, threatening the productivity of the grazing industry (Price et al., 2011). *Phyla nodiflora* var. *minor* grows either on dry soils or wetter areas.

Phenology. Flowering was documented mainly between September and March, but in the northernmost distributional area, the taxon was found in flower in August.

Taxonomic notes. *Phyla nodiflora* var. *minor* is distinguished principally by its small, elliptic to obovate leaf blades, with an acute apex, as well as the white strigose pubescence on the leaves and stems, which are often densely canescent. *Phyla nodiflora* var. *nodiflora* has bigger spatulate leaves (2–4[–7.5] × 0.5–1.5[–3] cm vs. 0.5–2[–4] × 0.2–1 cm), with a mostly subobtuse apex and pubescence that is slightly adpressed strigose or glabrescent, and never canescent. Furthermore, *P. nodiflora* var. *minor* has mauve or white, fading to pink or lilac flowers, while in the typical variety the flowers are generally white.

Acevedo (1951) described *Phyla nodiflora* f. *copiapina* on the basis of its numerous leaves and florescences with whitish pubescence. Our examination of the type material of this taxon indicates that it corresponds to *P. nodiflora* var. *minor*, sharing its canescent pubescence and leaf blade size.

Selected specimens examined. MEXICO. **Hidalgo:** 1971, *Spellman 954* (MO). HAITI. **Sud:** Etang, *Leonard 3487* (US). U.S.A. **California:** San Joaquín, *Wolff 2840* (MO). DOMINICAN REPUBLIC. **Monte Cristi:** Monción, *Valeur 447* (US). ARGENTINA. **Buenos Aires:** Chapadmalal, *Hicken 476* (SI); San Fernando, Pachecho, *Boelcke 6676* (SI). **Catamarca:** El Alto, *Kiesling 1273* (SI). **Chaco:** Gral. Güemes, *Fortunato 1273* (SI). **Chubut:** Paso de los Indios, *Arroyo 59* (SI). **Córdoba:** San Esteban, *Nicora 1637* (SI). **Corrientes:** Mburucuyá, Ea. Sta. Teresa, *Pedersen 1873* (US). **Entre Ríos:** Gualeguaychú, Ea. Las Casuarinas, *Romanczuk 10* (SI). **Formosa:** Bermejo, *Fortunato 4547* (MO). **Jujuy:** Tumbaya, *Venturi 4903* (MO, SI, US). **La Pampa:** Hucal, Abramo, *Kaufmann 4949* (SI). **La Rioja:** Gral Ocampo, *Biurrum 1599* (SI). **Mendoza:** Tupungato, *Ruiz Leal 2172* (SI). **Neuquén:** Zapala, Covunco, *Perez Moreau 3419* (SI). **Río Negro:** San Antonio, *Correa 10135* (SI). **Salta:** La Viña, *Novara 8511* (SI). **San Juan:** Sarmiento, Lagunas de Guanacache, *Kiesling 5043* (SI). **San Luis:** Paso de las Carretas, *Vignati 7020* (SI). **Santa Fe:** Garay, Ao. El Potrero, *Fossati 706* (SI). **Santiago del Estero:** Fortin Tostado, June 1906, *Goubat s.n.* (SI). **Tucumán:** Tafí, Río de las Carreras, *Lillo 7633* (US). BOLIVIA. **Cochabamba:** Colina S. Pedro, 1960, *s. coll. 195* (US). **Santa Cruz:** Alto Mairana, *Steinbach 6038* (SI). BRAZIL. **Rio Grande do Sul:** Gravataí, Banhados do Pacheco, *Schultz 3492* (SI). CHILE. **Atacama:** Copiapó, *Cabrera 11378* (SI). **Biobío:** Concepción, Hualqui, *Junge 5927* (SI). **Coquimbo:** 1888, *Philippi 309* (US). **Los Ríos:** Valdivia, S. José de Mariquina, *Hollermayer 1196* (SI, US). **Maule:** Curicó, *Marticorena 838* (SI). **Santiago:** Batuco, *Hicken 887* (SI). **Valparaiso:** Simache, *Boelcke 409* (SI). ECUADOR. **Guayas:** Salinas, *Svenson 11164* (US). PARAGUAY. **Presidente Hayes:** 1994, *Zardini 40372* (MO). PERU. **La Libertad:** Huanchaco, *Straw 2404* (US). **Lambayeque:** Chiclayo, Pimentel, *Fosberg 27987* (US). **Lima:** Lomas Atocongo, *Velarde 582* (SI). URUGUAY. **Artigas:** 25 Nov. 2001, *Seijo 2432* (SI). **Lavalleja:** 29 Nov. 2001, *Seijo 2582* (SI). **Montevideo:** cuchilla Pereyra, *Felippone 3297* (SI). **Rocha:** Ao. Los Indios, *Burkart 21552* (SI). **San José:** Río Sta. Lucía, *Rosengurtt B 1399* (SI). EGYPT. **Cairo:** Kirdasa, 1975, *Helmy 10* (MO). ETHIOPIA. Harar, Lake Alemaya, *Burger 3440* (US). MOZAMBIQUE. **Maputo:** s. loc., 1909, *Howard 5* (US). SOUTH AFRICA. **Albany:** 1979, *Bayliss 8987* (MO). **Orange Free [Free State]:** Petrusburg, 25 Feb. 1981, *Herman 283* (US). FRANCE. **Aude:** Fleury, *Julien 4* (SI). **Hérault:** Periés, *Julien 1* (SI). SPAIN. **Málaga:** 1906, *Gandoger s.n.* (MO). AUSTRALIA. **New South Wales:** Heatherbrae, *Prichard 1* (SI). **Queensland:** St. Ruth's reserve, *Julien 6* (SI). **South Australia:** St. Austin Martin's Bend, 1983, *Symon 13087* (MO). **Victoria:** Derang Lakes, *Macdonald 1* (SI). CAROLINE ISLANDS. **Faraulap Atoll:** *Fosberg 47356* (US).

5c. Phyla nodiflora var. **reptans** (Kunth) Moldenke, Torreya 34(1): 9. 1934. Basionym: *Lippia reptans* Kunth, Nov. Gen. Sp. [H.B.K.] (quarto ed.) 2: 263. 1818. *Lippia nodiflora* var. *reptans* (Kunth) Kuntze, Revis. Gen. Pl. 2: 508. 1891. *Phyla reptans* (Kunth) Greene, Pittonia 4: 47. 1899. TYPE: Venezuela. Sucre: Cumana, Aug. 1800, *F. W. Humboldt & A. Bonpland 76* (holotype, P-307282 not seen, P-307282 photo at F-39483!; isotype, B-W-11120/1 not seen, B-W-11120/1 photo at SI!). Figure 4K, L.

Verbena fruticosa Mill., Gard. Dict., ed. 8: 14. 1768. *Lippia fruticosa* (Mill.) R. W. Sanders, Harvard Pap. Bot. 5: 347. 2001. *Phyla fruticosa* (Mill.) K. Kenn. ex Wunderlin & B. F. Hansen, Bot. Explor. (Florida) 3: 38. 2003. TYPE: Mexico. Campeche: s.d., *Miller s.n.* (holotype, BM not seen, BM photo at SI!).

Lippia queretarensis Kunth, Nov. Gen. Sp. [H. B. K.] (quarto ed.) 2: 264. 1818. TYPE: Mexico. Querétaro, *F. W. Humboldt & A. Bonpland 4196* (holotype, P not seen, P photo at SI!).

Lippia strigulosa M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11(2): 319. 1844. *Phyla strigulosa* (M. Martens & Galeotti) Moldenke, Phytologia 2: 233. 1947. *Lippia nodiflora* (L.) Michx. var. *strigulosa* (M. Martens & Galeotti) J. F. Macbr., Publ. Field. Mus. Nat. Hist., Bot. Ser. 13(5): 651. 1960. TYPE: Mexico. Veracruz: Antigua, June 1840, *H. Galeotti 748*

(holotype, BR not seen, BR photo at SI!; isotype, P not seen, P photo at SI!).

Lippia nodiflora f. *sericea* Kuntze, Revis. Gen. Pl. 2: 508. 1891. *Phyla nodiflora* var. *sericea* (Kuntze) Moldenke, Phytologia 1: 98. 1934. *Phyla strigulosa* var. *sericea* (Kuntze) Moldenke, Phytologia 19: 435. 1970. TYPE: Trinidad and Tobago: Trinidad, 4 Apr. 1874, *O. Kuntze 714* (holotype, NY not seen, NY photo at SI!).

Phyla yucatana Moldenke, Phytologia 2: 140. 1946. TYPE: Belize. Corozal, Corozal–Pachacan rd., 20 July 1933, *P. H. Gentle & C. L. Lundell 4780* (holotype, NY not seen, NY photo at SI!; isotypes, CAS not seen, MICH not seen, MICH photo at SI!, NY [2] not seen, NY photo at SI!, TEX [3] not seen, TEX photo at SI!).

Phyla yucatana var. *parvifolia* Moldenke, Phytologia 2: 141. 1946. *Phyla strigulosa* var. *parvifolia* Moldenke, Phytologia 2: 233. 1947. TYPE: Mexico. Michoacán de Ocampo, Huetamo, Mal Paso, 9 May 1934, *G. B. Hinton 6024* (holotype, NY not seen, NY photo at SI!; isotypes, NY not seen, NY photo SI!, US not seen, US photo at SI!).

Plants 25–60 cm, stems erect, branches diffusely branching from the base; subglabrous or slightly adpressed strigose pubescence with malpighiaceous hairs. *Leaf* blade ovate to rhombic-ovate, 3–5(–8) × 1.5–3 cm, pinnate venation prominent abaxially, secondaries ending at the sinus of teeth; slightly adpressed strigose pubescence and malpighiaceous hairs abaxially; margins serrate with 8 to 10 pairs of acute teeth all along blade margin or toothed toward the distal part of the blade; apex acute. *Florescences* ovoid to oblong spikes, 1 × 1 cm at anthesis, elongating to 4–6(–7) cm at maturity; *corolla* pale blue, purple, or white, 4 mm long.

Distribution and habitat. *Phyla nodiflora* var. *reptans* is found only in the Americas: in North America (United States and Mexico), Central America (Belize, Costa Rica, El Salvador, Guatemala, Honduras, and Puerto Rico), the Antilles (Anguilla, Barbados, Cuba, Dominican Republic, Guadaloupe, Haiti, Jamaica, Martinique, and the Virgin Islands), and in South America (Argentina, Bolivia, Brazil, Colombia, Curaçao, Ecuador, Paraguay, Peru, and Venezuela). *Phyla nodiflora* var. *reptans* was collected from wet forested areas, riverbanks, or open fields with wet soil.

Phenology. This taxon was collected in flower in all seasons except winter.

Taxonomic notes. *Phyla nodiflora* var. *reptans* is principally distinguished by its ovate to rhombic-ovate leaf blades with an acute apex, serrate margins or at least distally toothed, and a conspicuous pinnate venation abaxially. In *P. nodiflora* var. *nodiflora* and *P. nodiflora* var. *minor*, the leaf blades are elliptic to obovate, but never ovate, with a subobtuse or an acute apex. The blade margins are entire or distally serrate, with venation abaxially indistinguishable, and generally only the midvein prominent.

Selected specimens examined. MEXICO. **Campeche:** s. loc., 1996, *P. Alvaro M. 276* (MO). **Chiapas:** s. loc., 1960, *Merrill King 2761* (US). **Coahuila:** Saltillo, *Arsène 3423* (US). **Hidalgo:** s. loc., 1937, *Fisher 3773* (US). **México:** DF, *Hinton 4343* (US). **Michoacán:** Morelia, *Arsène 2792* (US); Morelia, s. loc., 1909, *Arsène s.n.* (US). **Nuevo León:** s. loc., 1972, *Dziekanowski 1752* (US). **Oaxaca:** s. loc., 1894, *Nelson 336* (US). **Puebla:** s. loc., 1906, *Arsène 407* (US). **Querétaro:** s. loc., 1910, *Arsène 10253* (US). **San Luis Potosí:** Charcas, *Lundell 5181* (US). **Sinaloa:** s. loc., 1904, *Brandegee s.n.* (US). **Sonora:** s. loc., 1934, *Studhalte 1541* (US). **Tabasco:** Centla, *Novelo 1951* (MO). **Tamaulipas:** s. loc., *Merrill King 3818* (US). **Veracruz:** s. loc., 1910, *Orcutt 2985* (US). **Yucatán:** s. loc., 1917, *Gaumer 23670* (US). U.S.A. **Florida:** Dade, *Avery 1530* (MO). **New Mexico:** Eddy, *Standley 40452* (MO). **Texas:** La Joya, *Walker 70* (MO). LESSER ANTILLES. **Anguilla:** s. loc., 1959, *Proctor 18677* (US). BARBADOS. s. loc., 1906, *Dash 137* (US). BELIZE. **Cayo:** Georgeville, *Sorensen 7116* (US). **Orange Walk:** Honey camp, *Lundell 553* (US). COSTA RICA. s. loc., 1965, *Jimenez 3095* (US). CUBA. **Guantánamo:** s. loc., 1997, *Axelrod 10439* (MO). **La Habana:** El Rosario, *Juzepczuk 4078a* (US). **Pinar del Río:** s. loc., 1990, *Gentry 71384* (MO). **Sancti Spíritus:** s. loc., 1993, *Acevedo Rodriguez 5503* (US). **Villa Clara:** Santa Clara, *Smith 3124* (US). DOMINICAN REPUBLIC. **Azua:** Santo Domingo, *Rose 4011* (US). **Monte Cristi:** s. loc., 1921, *Abbott 1008* (US). EL SALVADOR. **San Miguel:** s. loc., 1922, *Standley 20994* (US). GUATEMALA. **Alta Verapaz:** Coban, *Turckheim 1259* (SI). **Izabal:** s. loc., 1922, *Standley 24637* (US). **Petén:** s. loc., 1942, *Steyermark 45930* (US). HAITI. **Nord-Ouest:** Baie des Moustiques, *Leonard 11800* (US). HONDURAS. **Atlántida:** s. loc., 1928, *Standley 55765* (US). **Comayagua:** s. loc., 1964, *Standley 14266* (US). **Santa Bárbara:** s. loc., 1888, *Thieme 5407* (US). **Yoro:** s. loc., 1928, *Standley 55007* (US). JAMAICA. **Saint Ann:** s. loc., 1960, *Adams 6718* (MO). MARTINIQUE. **Sainte-Anne:** s. loc., 1945, *Stehlé 6179* (US). PUERTO RICO. Montalva, s. loc., 1915, *Britton 4799* (US). Puerto Rico, Fajardo, *Britton 1596* (US). U.S. VIRGIN ISLANDS. **St. Croix:** *Ricksecker 223* (MO). ARGENTINA. **Buenos Aires:** Barrancas CABA, Apr. 1918, *Molfino s.n.* (SI). **Chaco:** Riacho Salado, Oct. 1987, *Hernonen s.n.* (SI). **Corrientes:** Gral. Paz, *Vanni 88* (SI). **Entre Ríos:** La Paz, *Burkart 30125* (SI). **Formosa:** Pirané, *Guaglianone 663* (SI). **Jujuy:** Santa Bárbara, *Morrone 4479* (SI). **Salta:** Orán, río Blanco, *Venturi 5577* (BM, SI, US). **Santiago del Estero:** s. loc., *Lillo 72* (US). **Tucumán:** Famaillá, Quebrada Leales, *Venturi 2304* (SI). BOLIVIA. **Santa Cruz:** entre Guabira y Portachuelo, *Zuloaga 1481* (SI); Jara, entre Nueva Motea y Portachuelo, *Steinbach 2888* (SI). **Tarija:** O'Connor, *Beck 9682* (SI). BRAZIL. **Mato Grosso do Sul:** Bonito, Guaicurus, *Hatschbach 76114* (SI). COLOMBIA. **Atlántico:** Barranquilla, *Elias 141* (US). **La Guajira:** Maicao, *Roldán 1024a* (MO). **Valle del Cauca:** Riofrio, *Silverstone 867* (MO). CURAÇAO (NETHERLANDS). Shalome, s. loc., 1952, *Arnoldo 2051* (US). ECUADOR. **Galápagos Islands:** Kreck Bay, *Stewart 3302* (SI). **Guayas:** Guayaquil, *Stork 8977* (US). **Manabí:** San Jacinto, *Roig 9853* (SI). PARAGUAY. **Alto Paraguay:** Cerro León, Laguna Nueva Misión, *Schinini 18015* (G). **Boquerón:** Tinfunké, *Mereles 521* (SI). **Central:** lago Ypacarai, *Hassler 11567* (BM, US).

Concepción: s. loc., 1901–1902, *Hassler 7438* (BM, G). **Ñeembucú:** Cerrito, *Hassler 1338* (BM, G). **Presidente Hayes:** Ea. Zalazar, *Zardini 45976* (SI). PERU. **La Libertad:** s. loc., 1934, *Graywood Smyth 28* (US). **Lambayeque:** de Chiclayo a Reque, *Scolnik 1244* (SI). **Lima:** s. loc., 1976, *Gentry 16457* (MO). **Piura:** s. loc., 1955, *Böcher 278* (US). **San Martín:** s. loc., 1937, *Belshaw 3168* (US). **Tumbes:** s. loc., 1968, *Simpson 583* (US). VENEZUELA. **Anzoátegui:** Bruzual, *Delascio 12902* (MO). **Carabobo:** Pto. Cabello & El Patito, *Pittier 8782* (SI). **Falcón:** Paraguaná, Pueblo Nuevo, *Tamayo 1091* (US). **Lara:** El Tocuyo, *Tamayo 3353* (SI). **Mérida:** Playa de Cabo Blanco, *Pittier 10187* (US). **Nueva Esparta:** Isla de Margarita, *Steyermark 130972* (MO).

Incertae Taxa

Walpers (1845: 49) mentioned four varieties of *Phyla nodiflora* (sub nom. *Lippia nodiflora*), as *L. nodiflora* var. *arenaria* Walp., *L. nodiflora* var. *debilis* Walp., *L. nodiflora* var. *vulgaris* Walp., and *L. nodiflora* var. *umbrosa* Walp. No specimen information was cited and the location of Walpers's types is unknown (Stafleu & Cowan, 1988). A similar situation occurred with another taxon by Walpers whose type material was not found (*L. uncinuligera* Nees ex Walp., Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19, Suppl. 1: 377. 1843. TYPE: Chile, Melipilla, s.d, *s. coll.*). The fact that this last specimen is from Chile makes it probable that it might be a synonym of *P. nodiflora*, but the absence of type material makes it impossible to ascertain.

Lippia nodiflora f. *brevipes* Kuntze, Revis. Gen. Pl. 2: 508. 1891. TYPE: Java: Samarang, Bombay.

The type material of this taxon has not been located and is not housed in NY. It may be related to *Phyla nodiflora* var. *nodiflora* since this taxon is the only one known to be distributed in Java.

Lippia litoralis Phil., Anales Univ. Chile 90: 624. 1895. TYPE: Chile. Constitución, "in litore arenoso ad Constitucion," 1885–86, *P. Ortega s.n.*

The type material of this taxon was not found in the herbaria at SGO or P. In his protologue, Philippi mentions its similarity to *Lippia canescens* Kunth [= *Phyla nodiflora* var. *minor* (Hook.) N. O'Leary & Múlgura].

Lippia nodiflora f. *pseudo-sarmentosa* A. Reyn., Bull. Soc. Bot. Fr. 62: 205. 1915.

No type material was found for this taxon, with collections investigated at FI, G, and NICE.

Excluded Taxa

The following two taxa, *Lippia dulcis* Trevir. and *L. stochaedifolia* (L.) Kunth, were treated by three previous authors under *Phyla* (López Palacios, 1977; Pool, 2001; Méndez Santos, 2003). However, these are considered here to be better placed under *Lippia*, given that both species lack malpighiaceous hairs, which are characteristic of the genus *Phyla*, and are woody shrubs rather than the herbaceous habit noted for all *Phyla* species considered herein. Phylogenetic studies (Marx et al., 2010) show that both taxa lie within a *Lippia* clade and are not nested within the five *Phyla* taxa sampled.

Lippia dulcis Trevir., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 13(1): 187. 1824. *Phyla dulcis* (Trevir.) Moldenke, Torreya 34: 9. 1934. TYPE: Cuba. Cultivated from seed sent by Antonius de la Ossa, grown in the garden of George Staunton, s.d., *s.n.* (holotype, BHU not seen; isotype, NY not seen, NY photo at SI!).

Verbena stoechadifolia L., Sp. Pl. 1: 19. 1753. *Zappania stoechadifolia* (L.) Juss., Pers. Syn. Pl. 2: 140. 1806. *Lippia stoechadifolia* (L.) Kunth, Nov. Gen. Sp. [H.B.K.] (quarto ed.) 2: 265. 1817 [1818]. *Panope stoechadifolia* (L.) Raf., Fl. Tellur. 2: 103. 1836. *Phyla stoechadifolia* (L.) Small, Bull. Torrey Bot. Club 36: 162. 1909. TYPE: Herb. A. van Royen 913. 13–121 (neotype, designated by Méndez & Cafferty [2001: 1140], L not seen, L photo at SI!).

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Appendix 1. List of species and index to collectors. Collections are listed alphabetically by the collector's last name. The number in parentheses, after the collector's number, corresponds to the species number in the species list. Specimens are located in BM, G, MO, NY, SI, and US.

1. *Phyla betulifolia* (Kunth) Greene
2. *Phyla cuneifolia* (Torr.) Greene
3. *Phyla lanceolata* (Michx.) Greene
4. *Phyla linearis* (Kunth) Tronc. & López-Pal.

5a. *Phyla nodiflora* (L.) Greene var. *nodiflora*

5b. *Phyla nodiflora* (L.) Greene var. *minor* (Hook.) N. O'Leary & Múlgura

5c. *Phyla nodiflora* (L.) Greene var. *reptans* (Kunth) Moldenke

Abbott 1008 (5c), 1766 (5a), 2869 (5a); **Abrams** 2527 (3); **Acevedo Rodriguez** 5503 (5c); **Adams** 6718 (5c); **Ahumada**

4625 (5c), 8489 (5c), 8804 (5c), 8977 (5b); **Albert** 2090 (2); **Allard** 14765 (5a), 14780 (5a); **Allison** 132 (3), 278 (5a); **Alston** 6360 (5c); **Alvarez** 507 (5b); **Andriamihajarivo** 821 (5a); **Antuña** 72 (5c); **Apollinaire** s.n. (5a); **Arbo** 247 (5b), 8941 (5c); **Archer** 1402 (1); **Arenas** 2256 (5c), 3091 (5a); **Armer** 5532 (5c); **Arndt** 19 (5a); **Arnoldo** 2051 (5c); **Arroyo** 59 (5b); **Arsène** s.n. (5a), s.n. (5c), 92 (5c), 407 (5c), 936 (5a), 2792 (5c), 3423 (5c), 6334 (5a), 8532 (5c), 10253 (5c), 10366 (5c); **Asplund** 111 (5a), 5641 (5b), 11105 (5a), 13890 (5c), 14293 (1); **Avery** 1530 (5c); **Aweke** 2442 (5a), 2445 (5a); **Axelrod** 10439 (5c).

Babcock s.n. (3); **Bacigalupo** 11658 (5b); **Bailey** 1616 (1); **Baker** 287 (5c), 1439 (5a); **Bakery Van Herman** 1964 (5a); **Bakery Wilson** 2230 (5a); **Baldwin** 5738 (5a); **Ball** 419 (5a); **Baltars** 2768 (3); **Barclay** 402 (5c); **Barrell** 162–73 (3); **Barren** s.n. (3); **Bartlett** 16371 (1), 19691 (5b); **Bartsch** s.n. (3); **Bastión** 297 (5a); **Bayliss** 8987 (5b); **Bayliss-Smith** 16 (5a); **Bazzi** 345 (5c); **Bechdolt** s.n. (3); **Beck** 6462 (5c), 9682 (5c), 11517 (5c), 11594 (5c), 19525 (1), 20455 (1); **Belshaw** 3168 (5c); **Bentley** 274 (5a); **Berlandier** 316 (5a); **Bernard** 497 (5b); **Bernardi** 15673 (5a); **Biurrum** 1599 (5b); **Böcher** 278 (5c); **Bodenheim** 5235 (5a); **Boelcke** 409 (5b), 1532 (5b), 5046 (5b), 6676 (5b); **Bogusch** 11915 (5c); **Boom** 7194 (1); **Bourgeau** 548 (5a); **Bowes** 29 (5b); **Brace** 5208 (5a); **Bradley** 1215 (5a); **Brandegee** s.n. (5c); **Brass** 17998 (5a), 28665 (5a); **Braun** s.n. (3), 1716 (3), 2519 (3), 3170 (3), 4056 (3); **Braunton** 447 (3), 499 (3), 627 (3); **Breteler** 4359 (5c); **Brinker** 370 (5a); **Britton** 1055 (1), 1596 (5c), 4799 (5c), 14520 (5a), 15400 (5a); **Brizuela** 1463 (5b); **Broadway** s.n. (1), 7206 (1), 8954 (1); **Brooks** 7 (5a), 17773 (5a); **Bruner** s.n. (3); **Buchanan** 339 (5a); **Buchtien** s.n. (5b), 12354 (5a); **Bunger** 409 (5a); **Burcham** 176 (5a); **Burger** 3440 (5b); **Burkart** 468 (5b), 3964 (5b), 4489 (5b), 6791 (5c), 8356 (5b), 8434 (5a), 9345 (5b), 13198 (5a), 16333 (5a), 20220 (5a), 21552 (5b), 21555 (5a), 23096 (5b), 23794 (5b), 24906 (5b), 25147 (5a), 27049 (5c), 27053 (5c), 27054 (5c), 27361 (5b), 28073 (5b), 28976 (5b), 30100 (5b), 30124 (5c), 30125 (5c), 30127 (5c), 30602 (5a); **Bush** 471 (5a), 1412 (5a), 4070 (3).

Cabral 741 (5a); **Cabrera** 2130 (5b), 4247 (5b), 9860 (5b), 11378 (5b), 13610 (5a), 20075 (5a), 20269 (5c), 23549 (5b), 24028 (5c), 27550 (5c), 27562 (5b), 29674 (5b), 29861 (5c), 32242 (5c), 33626 (5c), 34568 (5b), 34617 (5b); **Calderón** 2380 (5c); **Camp** E-3549 (5c); **Canby** 841 (3), 2665 (3); **Cantino** 391 (5c); **Carrington** 1867 (5a); **Cerón** 6711 (5c); **Cerrate** 1624 (5a); **Chalukian** 1995 (5b); **Chandler** s.n. (3), 7012 (5c), 7012a (5c); **Chase** 7724 (5a); **Clarke** 3861 (1); **Clemente** 4451 (5c); **Clewel** 2595 (5a); **Collins** 264 (5a); **Colonnello** 1806 (1); **Congdon** s.n. (3); **Copeland** 3501 (5b); **Correa** 6 (5b), 7701 (5c), 10130 (5b), 10135 (5b), 10521 (5b); **Correll** 14945 (5c), 48746 (5a); **Corwen** s.n. (2), 402 (2); **Cory** 53264 (3); **Crandall** s.n. (2); **Crawford** s.n. (3); **Crespo** 1808 (5b); **Croat** 2455 (5a), 19147 (1), 23646 (5c); **Cuezzo** 1743 (5a); **Cunquero** 331 (5b); **Curtiss** 706 (5a).

Daniels 406 (2); **Darbyshire** 805 (5a); **D'Arcy** 2014 (5a), 15292 (5a); **Dash** 137 (5c); **Davidson** 232 (3); **Davis** 55600 (5a); **Dawson** 1640 (5a), 26764 (5a), 26770 (5a), 26855 (5a); **Deam** 1195 (3), 60610 (5a); **Decary** 12873 (5a); **Degen** 2962 (5a); **Degener** 35075 (5a); **Deguchi** 6344 (5a); **Delascio** 12902 (5c); **Demaree** 6943 (3), 8355 (3), 11445 (3), 14087 (3), 17288 (5a); **Dillon** 4753 (5a); **Dodge** 99 (5c); **Dodson** 12978 (5c); **Donnell Smith** s.n. (3); **Dorr** 941 (5a), 3309 (5a); **Dowell** 4172 (1); **Drake** 114 (5a), 918 (5a); **Drake** s.n. (5a), s.n. (5c); **Drummond** 254 (3); **Duarte** 7317 (1); **Duke** 4328 (5a), 9663 (5a); **Duss** 2941 (5a), 415 (5a); **Dwyer** 2500 (5a), 13638 (5a), 15056 (5a); **Dziekanowski** 1752 (5c).

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- ☐ To indicate ranges of numbers, for example, page numbers, 20–23; measurements, 5–7 mm; altitudes, 1500–2500 m, insert an en dash from the Word symbol menu.
- ☐ A single hyphen is used in hyphenated words, for example, 9-nerved, oval-triangular.
- ☐ Common Latin words or phrases are not italicized (e.g., et al., i.e., sensu, etc.).
- ☐ Only taxon names at the rank of genus and below are italicized.
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- ☐ *Chicago Manual of Style*, latest edition, is used as a reference.

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- ☐ Footnotes are typed as double-spaced paragraphs on the first page. The first footnote contains acknowledgments, including information on granting agencies, herbaria that loaned specimens, and the name of the artist. The second footnote is the author's address. Addresses for additional authors are each

separate footnotes. No other footnotes occur, except in tables.

5. Abstract & Key Words

☐ A one-paragraph abstract precedes the text. Papers in Spanish have an English abstract in addition to a Spanish resumen.

☐ The abstract is concise (1 paragraph) and includes brief statements about the paper's intent, materials and methods, results, and significance of findings.

☐ A brief list of key words immediately follows the abstract.

6. Taxonomic Treatment

☐ Species entries are organized as follows: Heading, vernacular name(s), Latin or English diagnosis (if necessary), description, distribution, summary, discussion, specimens examined. The discussions are parallel and follow the same order, e.g., diagnostic characteristics, distinction from similar species variation, distribution and ecology, nomenclature and typification, uses.

☐ One paragraph per basionym is used as follows: Taxon author, literature citation, type citation, e.g., *Beilschmiedia latifolia* (Nees) Sa. Nishida, Ann. Missouri Bot. Gard. 86: 680. 1999. *Hufelandia latifolia* Nees, Syst. Laur.: 674. 1836. TYPE: Peru. Locality not indicated, 1835 (fl.), *Matthew 1433* (holotype, E!; isotypes, BM!, E!, K!, LE not seen, OXF not seen).

☐ Synonyms based on different types are placed in separate paragraphs, each beginning with the basionym, followed by other combinations (if appropriate), and citation of the type.

☐ A Latin or English diagnosis for each new taxon is provided, immediately following the new taxon's name and type designation and immediately preceding the English or Spanish description of the new taxon. The *International Code of Nomenclature for Algae, Fungi and Plants* (Glossary) defines a diagnosis of a taxon as "a statement of that which in the opinion of its author distinguishes the taxon from other taxa." The journal's suggested style for the Latin diagnosis of a new species might include "Haec species . . . affinis [similis], sed ab ea [eo] . . . distinguitur [differ]," or in place of "Haec species" beginning with "Species nova" or equivalent wording. Suggested style for the English diagnosis of a new species might include "This [new] species is related [similar] to . . . , but is distinguished [differs] from it by . . ." or equivalent wording. Reference to diagnostic characters elsewhere in the text (abstract, discussion, key, etc.) is not acceptable in place of the formal diagnosis.

☐ For species with infraspecific taxa: Description and discussion are composite (incorporating all infraspecific taxa) and parallel with other species descriptions. Descriptions of infraspecific taxa are parallel with one another (in the same species). All synonyms are listed under the appropriate infraspecific taxon.

☐ Descriptions: Descriptions are parallel, within a given rank. All measurements are metric. Hyphens are used for parenthetical extremes: "peduncle (8.2–) 14.3–28.0(–31.9) cm long," unless intermediate values are not expected: ovary with (2)4(6) locules. Length × width are given in the following manner: lamina 36.4–82.8 × 9.1–16.8 cm.

☐ When relevant, nomina nuda, misapplied names, and superfluous names are included in the discussion following the description, but are not part of the formal synonymy.

7. Citation of Types

☐ Exclamation points are used for specimens examined, and types not seen are indicated as such (e.g., MO!, US not seen).

☐ Lectotype designations are included together with an indication of where they were designated [author, year, page number, and herbarium of deposition; e.g., *C. J. W. Schiede 159* (lectotype, designated by Stevens [2000: 256], P!; isotypes. . .)]. This reference is listed in the Literature Cited. If the author of the paper submitted is making the lectotypification, the phrase "designated here" is used.

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☐ Create tables using the Microsoft Word "Table" feature.

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☐ Each table starts on a separate page.

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☐ Periods are used after all abbreviations (which are minimized) except metric measures, compass directions, and herbarium designations.

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☐ Periodicals are abbreviated according to *B-P-H* (*Botanico-Periodicum-Huntianum*) and to *B-P-H/S* (*Botanico-Periodicum-Huntianum/Supplementum*).

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☐ Book titles are abbreviated according to *Taxonomic Literature, edition 2*, but with initial letters capitalized. Book titles are spelled out in the Literature Cited.

☐ If an item does not appear in *B-P-H* or *TL-2*, or if these references are not available, its title is fully spelled out.

☐ Herbaria are abbreviated according to the most recent edition of *Index Herbariorum*.

☐ Abbreviated forms are not used for references in the text, except when citing the names of plants. If it is necessary to cite a particular page in the text, the form Smith (1998: 12) is used.

10. Specimens Examined

☐ If many specimens were examined, those cited in the text are limited to ca. 12 manuscript pages.

☐ If there are a large number, an index to specimens examined is placed at the end of the paper, following the Literature Cited. It is arranged alphabetically by collector, followed by collection number, followed by the number of the taxon in the text. Names (including initial(s)) of first and second collector are provided, "et al." if three or more.

☐ Specimens are cited in the text as follows: *Additional specimens examined* (or *Selected specimens examined*). MEXICO. **Oaxaca:** Sierra San Pedro Nolesco, Talea, 12°37′N, 85°14′W, 950–1100 m, 3 Feb. 1987 (fl), *Jergensen 865* (BM, G, K, US). [Dates and reproductive status are optional but are omitted from longer lists.] Countries are run together in the same paragraph, e.g., COUNTRY A. **Major political division:** . . . COUNTRY B. **Major political division:** . . . Separate paragraphs are used for major continental regions within major political divisions.

11. Specimen Vouchers and Genetic Sequences

☐ If the paper presents original data, associated herbarium vouchers are cited. [Vouchers for seed and/or other collections should be included where pertinent. Dependent on the paper, reference to the original wild source may be required.] Vouchers are also cited from common names, and uses are taken from specimen labels.

☐ Herbarium vouchers state the collector and number, herbarium in which the voucher is located, and a clear annotation that the material represents the voucher for the study in question.

☐ Nucleic acid or protein sequences corresponding to equal or greater than 50 nucleotides are entered into an appropriate data bank, e.g., GenBank/EMBL. The accession numbers are provided before publication. [Long sequences (exceeding two pages) will not be routinely published.]

☐ Data sequences and tree files should be provided in Nexus format or alternatively submitted to the TreeBASE web site (<www.treebase.org>).

☐ Author accepts responsibility for establishing the accuracy of information provided.

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☐ Keys are clear and have been checked carefully for consistency with the descriptions. Leads of each couplet are parallel.

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☐ Infraspecific taxa are keyed separately, not in species keys.

13. Literature Cited

☐ The Literature Cited contains full citations of all references cited in the text.

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☐ Spelling of author(s) name(s) and years of publication have been double-checked.

☐ All entries have been verified against original sources, especially journal titles, accents, diacritical marks, and spelling in languages other than English.

☐ Periodicals are listed as follows: author's last name, initial(s). Year. Full title of article. Journal abbreviated as in *B-P-H/S*. Volume: pages. No parenthetical part numbers after volume numbers are given unless each part is paginated separately.

☐ For more than one author, this style is followed: author's last name, initial(s), second author's initial(s), last name & third author's initial(s), last name.

☐ Books appear as follows: author's last name, initial(s). Year. Full Unabbreviated Title (edited by Editor), 3rd ed., Vol. 2. Publisher, City of Publication.

☐ For an article within a larger work, this style is followed: Author(s). Year. Name of the article. Pp. 00–00 *in* Name of the editor(s), Full Title of Larger Work. Publisher, City of Publication.

☐ Citations of work "in prep.," unpublished theses and dissertations, and similar references to inaccessible sources have been eliminated or kept to a minimum. They are not necessarily included in the Literature Cited.

14. Illustrations

☐ Electronic figures are labeled with the first author's last name, the first four letters of the taxon, and "...Figure1.tif", "...Figure2.tif", etc. The file extension clearly indicates what type of file it is.

☐ Scale bars appear on illustrations, photographs, and maps.

☐ Magnifications/reductions are not indicated in captions.

☐ Electronic scans may be pre-sized to fit either column width (2-5/8 in. or ca. 68 mm) or full-page width (5-1/2 in. or ca. 140 mm). [Maximum size for printed illustrations is 5-1/2 × 8-1/4 in.]

☐ Figures are numbered in Arabic numerals in the order of their citation in the text. Parts of figures are labeled with capital letters.

☐ Text in figures is in Times New Roman.

☐ Photographs are prepared according to the printer's requirements. [See Guide to Digital Art, Allen Press through the Publication Submission link on the opening page of http://www.mbgpress.info/.]

☐ Figures are grouped into composite plates when possible; edges of photographs are abutted.

☐ Edges of figures are squared.

☐ Maps include reference to latitude and longitude and are bounded by a fine border.

☐ Scanning electron micrographs are free of conspicuous charging.

☐ Axes on graphs are all labeled.

☐ Captions provide all explanatory text. Captions are separate from other text, one paragraph for each group of figures, and following the style in current issues of the *Annals*.

☐ Symbols on maps are legible, and reduction has been taken into consideration.

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